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MOSAIC and STREAK VIRUSES of the Potato

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MOSAIC and STREAK VIRUSES of the Potato

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RESEARCH BRANCH
CANADA DEPARTMENT OF AGRICULTURE

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INTRODUCTION

This publication gives information on eight viruses and their strains that produce symptoms of mosaic or streak in the potato. Each virus is discussed in a separate chapter. Descriptions are given of the properties of each, the mode of transmission, the symptoms produced in some of the varieties of potatoes registered or grown in Canada and the characteristic symptoms induced in plants used in diagnosis. The plants known to be susceptible to each virus are listed, and the solanums that are known to be immune or highly resistant. A selected list of references is given at the end of each chapter. By use of the accepted code letters and English popular names, controversial nomenclature is avoided. A list of synonyms is included to aid the reader in associating the viruses with some of the names used for them in the literature. The information is useful to the student of potato viruses, to those concerned with identification of potato virus diseases and to the geneticist who is searching for potatoes immune or resistant to some of the important viruses described.

Grateful thanks are due the following for valuable suggestions and criticism: Mr. I. L. Conners, Research Branch, Ottawa; Dr. N. S. Wright, Research Station, Vancouver; and Dr. R. H. E. Bradley and Mr. James Munro, Research Station, Fredericton. Dr. M. E. MacGillivray and Mr. Leo A. Dionne, Research Station, Fredericton, checked the names of insects and plants respectively. Special thanks are due Dr. R. H. Bagnall, Research Station, Fredericton, for providing photographs for several of the illustrations and much valuable criticism of the chapters on viruses F, M and S.

VIRUS A

SYNONYMS

Supermild mosaic virus, Quanjer; potato mild mosaic virus, Schultz & Folsom; potato virus A, Murphy & McKay; *Solanum virus* 3, Smith; *Marmor solani,* Holmes; *Solanum virus parvathermus,* Roland; *Solanum virus alphaicum,* Köhler.

HOST RANGE

SOLANACEAE: *Datura ferox* L., *D. metel* L., *D. stramonium* L., *Hyoscyamus albus* L., *H. aureus* L., *H. canariensis* L., *Lycopersicum pimpinellifolium* Mill., *Lycium viscosa* Link, *L. barbarum* L., *L. halimifolium* Mill., *L. rhombifolium* (Moench.) Dipp., *Nicandra physalodes* (L.) Pers., *Nicotiana alata* Link & Otto, *N. alba* Mill., *N. angustifolia* Mill., *N. fragrans* Hook., *N. gigantea* Ledeb., *N. glauca* Grah., *N. glutinosa* L., *N. langsdorfii* Weinm., *N. longiflora* Cav., *N. paniculata* L., *N. petiolaris* Schleich., *N. plumbaginifolia* Viv., *N. quadrivalvis* Pursh, *N. sanderae* Sander., *N. sylvestris* Spegaz. & Comes, *N. tabacum* L., *N. viscosa* Link, *Petunia axillaris* (Lam.) B.S.P., *P. hybrida* Vilm., *P. inflata* Juss., P. *nyctaginiflora* Juss., *Physalis minima* L., *P. philadelphica* Lam., *Salpiglossis sinuata* Ruiz & Pav., *Solanum andigenum* Juz. & Buk., *S. bukasovii* Juz., *S. Capsicastrum* Link, *S. citrullifolium* A. Br., *S. demissum* Lindl., *S. demissum* var. *klotzschii* Bitt., *S. demissum* var. *xitlense* Buk., *S. integrifolium* Poir., *S. miniatum* Bernh., *S. nigrum* L., var. *nodiflorum* L., *S. racemigerum* L., and *S. tuberosum* L.

TRANSMISSION

The virus is transmitted by sap inoculation, by stem and tuber graft and by the aphids *Aulacorthum solani* (Kltb.), *Aphis nasturtii* (Kltb.), *Macrosiphum euphorbiae* (Thom.) and *Myzus persicae* (Sulz.). The virus is nonpersistent (2, 8, 11).

PHYSICAL PROPERTIES

Most strains are inactivated by heating at 40° to 52° C. for 10 minutes (6). The dilution end point varies from 1:20 to 1:50 and the longevity in vitro varies from 18 to 24 hours at 20° C. (11). The particles are flexible threads with a normal length of 739 mμ and a diameter of 11 mμ (9).

IMMUNOLOGICAL AND SEROLOGICAL RELATIONSHIPS

Mild strains protect against the more virulent ones in susceptible hosts (6, 10). The virus is weakly antigenic. An antiserum has been prepared by using sap from *Nicotiana tabacum* that contained a high concentration of the virus (10). This test has been successful for the diagnosis of virus A in *N. tabacum* but not in potato (1).

INDICATOR HOSTS

Nicandra physalodes is useful for distinguishing virus A and its strains (6). The mild strain produces a vein clearing and slight stunting, the intermediate strain induces a vein clearing, diffused mottling and stunting, and the severe strain causes a distinct mottling, rugosity, necrosis and severe stunting.

Lycopersicum pimpinellifolium is also a useful plant for identifying virus A, especially when present in multiple infections with viruses X and Y (6, 14). The virus causes a necrotic flecking of the lower leaves, followed soon by a systemic necrosis. In some cases a marked epinasty of the petioles develops and the plants may die in about 12 to 14 days. Virus A also produces distinct blackish-brown local lesions on the leaves of *Solanum demissum* (Figure 1) (5, 15). Since somewhat similar lesions are produced by other viruses on this plant it is useful only when no other viruses are present.

Figure 1.—Local lesions in *Solanum demissum* caused by virus A. (R. H. Bagnall)

SYMPTOMS INDUCED IN POTATO

In susceptible varieties the virus alone incites a diffused faint or fleeting interveinal mottle (Figure 2), which is generally not visible under field conditions (12). In combination with strains of virus X, virus A produces a range of disorders commonly designated as mild mosaic (Figure 3), crinkle mosaic (Figure 4) and veinal mosaic (Figure 5) (8, 13). Such symptoms are produced in Arran Victory, Bliss Triumph, Keswick, Green Mountain, Pontiac, President, Russet Burbank (Netted Gem), White Rose and a number of other varieties of North American and European origin. When viruses A, X and Y attack certain varieties simultaneously a severe crinkle mosaic is induced. The symptoms associated

Figures 2-5.—Mosaic symptoms in *Solanum tuberosum*. 2. Faint interveinal mottling in President induced by virus A. 3. Mild mosaic in Green Mountain caused by medium strains of viruses A and X combined. 4. Crinkle mosaic in Green Mountain induced by virulent strains of viruses A and X combined. 5. Early symptoms (veinal mosaic) in Green Mountain produced by viruses A and X combined.

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with these virus complexes vary according to the environment, the variety of potato infected and the strains of the combining viruses concerned. Generally the first symptom is a clearing of the veins, which is soon followed by an interveinal mottling that consists of partially green areas interspersed with normally green ones. When mild strains are involved the leaves generally remain flat and undistorted, but when medium and severe strains are combined there may be some deformity, unevenness of the leaf blade, crinkling and waviness of the margins and sometimes small necrotic spots in the interveinal areas. As the plant approaches maturity the stalks of infected plants may fall or lean outwards, whereas those of normal plants remain upright. The symptoms induced by combinations of viruses A, X and Y are more clearly defined when the temperature ranges from 16° to 18°C. But as the temperature rises the mottling may fade or disappear entirely, although the unevenness, crinkling and necrotic spots usually persist.

When virus A is introduced by grafting to certain varieties, a necrotic reaction called "top necrosis" is produced (2, 8). The earliest symptoms appear on the terminal leaves as chlorotic patches, which are soon replaced by larger areas of brownish necrotic tissue. This necrosis usually proceeds to the apex and spreads from the leaf to the petiole and the main stem, causing collapse and death of the affected shoot (Figure 6). Also, tubers from plants that show top necrosis are necrotic on the surface and in the interior (Figure 7). Externally the symptoms appear as depressed, irregular necrotic lesions, which may enlarge and coalesce and eventually cover most of the tuber surface, including the eyes. Internally there are dark necrotic lesions with central corky masses distributed through the pith and cortex. In severe cases the entire tuber is destroyed. If the tubers germinate they generally give rise to dwarfed necrotic plants (Figure 8) that rarely produce viable tubers. In such varieties as Irish Cobbler and Arran Crest, the reaction in the tuber is milder. Externally there is a slight necrosis surrounding the eyes and internally there are small brownish necrotic lesions irregularly dispersed in the pith and cortex (Figure 9) (7).

RESISTANT AND IMMUNE SOURCES

The top necrosis produced by virus A indicates hypersensitiveness to the virus, is inherited as a dominant character and is transmitted genetically (3, 4). This hypersensitiveness, which prevents systemic infection by the virus, is a valuable defence mechanism and, in the field, plants so constituted are rarely found infected with virus A. A number of varieties are hypersensitive to virus A, including the following: Abundance, British Queen, Canso, Craig's Defiance, Epicure, Duke of York, Great Scot, Irish Cobbler, Hindenburg, King Edward, Kerr's Pink, Up-to-Date and Saco.

Certain varieties that are susceptible to virus A when introduced by grafting and by sap inoculation can escape infection in the field. This property is genetically transmitted and is of significance in the practical control of the virus. Among the varieties that are capable of warding off infection by virus A in this manner are: Chippewa, Cherokee, Earlaine, Houma, Katahdin, Kennebec, Merrimac, Mohawk and Sebago.

Figures 6-9.—Resistant reactions to virus A in *Solanum tuberosum*. 6. Top necrosis in Up-to-Date, virus introduced by grafting. 7. External and internal necrosis in Up-to-Date tubers, virus introduced by grafting. 8. Dwarfed, necrotic Up-to-Date plants produced when tubers were infected with virus. 9. Round necrotic lesions in Irish Cobbler tubers.

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Certain lines of the following species of solanums are resistant to virus A: *Solanum acaule* Bitt., *S. tuberosum* ssp. *andigenum* (Juz. & Buk.) Hawkes, *S. chacoense* Bitt., *S. demissum, S. hougasii* Correl, *S. maglia* Schlechtd., *S. phureja* Juz. & Buk., *S. polyadenium* Greenm., *S. simplicifolium* Bitt., and *S. stoloniferum* Schlechtd. (16).

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VIRUS F

SYNONYMS

Potato aucuba mosaic virus, Quanjer; potato interveinal mosaic virus, Quanjer; potato pseudo-net-necrosis virus, Quanjer, Thung & Elze; potato tuber blotch virus, Clinch, Loughnane & Murphy; potato virus F, Clinch, Loughnane & Murphy; potato virus G, Clinch, Loughnane & Murphy; *Solanum virus* 8, Smith; *Solanum virus* 9, Smith; *Marmor aucuba,* Holmes.

This virus includes the viruses previously designated as tuber blotch virus (virus F), aucuba mosaic virus (virus G) (1, 5, 16, 18) and certain other forms recognized as strains of a common virus (14, 20).

HOST RANGE

AMARANTHACEAE: *Amaranthus retroflexus* L., *Celosia argentea* L., *Gomphrena globosa* L.; CARYOPHYLLACEAE: *Stellaria media* Vill.; CHENOPODIACEAE: *Chenopodium amaranticolor* Coste & Reyn.; FICOIDACEAE: *Tetragonia expansa* Murr.; LEGUMINOSAE: *Cyamopsis tetragonoloba* (L.) Taub., *Trifolium incarnatum* L., *T. subterraneum* L.; POLYGONACEAE: *Fagopyrum esculentum* Moench.; PORTULACACEAE: *Portulaca oleracea* L. var. *sativa* D. C.; SCROPHULARIACEAE: *Linaria maroccana* Hook.; SOLANACEAE: *Atropa belladonna* L., *Browallia elata* L., *Capsicum annuum* L., *Datura aegyptiaca* Vesl., *D. bernhardii* Lund., *D. fastuosa* L., *D. inermis* Jacq., *D. inoxia* Mill., *D. stramonium* L. var. *tatula* L., *Hyoscyamus niger* L., *Lycopersicum esculentum* Mill., *Nicandra physalodes* Gaertn., *Nicotiana affinis* T. Moore, *N. debneyi* Domin., *N. glauca* Grah., *N. glutinosa* L., *N. rustica* L., *N. sylvestris* Speg. & Comes, *N. tabacum* L., *Petunia hybrida* Vilm., *Physalis angulata* L., *P. floridana* Rydb., *P. peruviana* Rydb., *P. viscosa* Rydb., *Schizanthus wisetonensis* Hort., *Solanum aculeatissimum* Jacq., *S. andigenum* Juz. & Buk., S. *chacoense* Bitt., *S. demissum* Lindl., *S. dulcamara* L., *S. melongena* L., *S. nigrum* L., *S. nigrum* L. var. *nodiflorum* L., *S. sisymbriifolium* Lam., *S. racemosum* L., *S. tuberosum* L.

TRANSMISSION

The virus is transmitted by sap inoculation and stem graft to potato and a number of other solanaceous hosts (6, 22, 10). It is also transmitted by sap inoculation to certain nonsolanaceous plants (1.7). According to some authors (5, 19, 23) the virus is transmitted by aphids when viruses A and Y are present. The virus is spread slowly in the field by leaf contact (9).

PHYSICAL PROPERTIES

These properties vary slightly according to the strain involved. Most of the strains are inactivated by heating from 65° to 70°C. for 10 minutes. The

dilution end point ranges from 1:10,000 to 1:100,000 and the longevity in vitro varies from 60 to 90 days at 15° to 20°C. (5, 22). The particles of the virus are flexible threads 580 mμ long and 10-11 mμ wide (2, 15).

IMMUNOLOGICAL AND SEROLOGICAL RELATIONSHIPS

Weak strains of virus F protect potato and certain other solanaceous plants against invasion by the more virulent strains (6, 11).

The virus is strongly antigenic (3). A satisfactory antiserum has been prepared by using clarified sap of infected *Capsicum annuum, Datura stramonium* var. *tatula* and *Nicotiana tabacum* (1, 14).

This antiserum cannot be used satisfactorily for detecting virus F in potato sap. The best procedure is to transfer the virus to *Capsicum annuum* or *Datura stramonium* var. *tatula* and use the infected sap from these plants for the serological test (1).

INDICATOR HOSTS

Most strains of virus F produce distinctive symptoms in *Capsicum annuum* (1, 5, 10). Six to 10 days after introduction of the virus, light-gray concentric ring lesions 3 to 5 mm. in diameter appear on the inoculated leaves (Figure 10).

Figure 10.—Light-gray, ring-like lesions with brownish margins and vein clearing caused by virus F in *Capsicum annuum*.

Eventually these lesions become sunken necrotic spots with white or light-gray centers and brown or purple margins. Three to 5 days later the lower and middle leaves develop a vein clearing and elongated or ringlike necrotic lesions with brownish margins in the interveinal spaces. These leaves usually become malformed and bronzed; they curl downward, wither from the tip backward and fall off the plant. Young plants usually die but older ones may live for several weeks, defoliated except for a few dark-green apical leaves. Similar but less distinct symptoms are produced by strains of virus F in *Solanum nigrum* var. *nodiflorum*. The symptoms described above are more clearly defined when the temperature ranges from 20° to 22°C. When the temperature is lower, the virus usually does not become systemic but produces only local lesions. Since virus X produces somewhat similar symptoms in *Capsicum annuum* and *Solanum nigrum* var. *nodiflorum,* these plants cannot be used as indicator hosts when this virus is present. *Solanum miniatum* is also a useful diagnostic host for strains of virus F (11). The virus produces, in 6 to 7 days, light-gray rings and an etching of the veins of the inoculated leaves. These symptoms are followed by the appearance of gray or brown blotches on the middle and top leaves, which later become chlorotic, wither and fall off the plant.

SYMPTOMS INDUCED IN POTATO

Virus F occurs in a number of strains and, depending on the strain, incites a variety of symptoms in potato (4, 6, 11, 14, 17, 21). Some strains produce no symptoms in the following varieties: Albion, Arran Crest, Canso, Chippewa, Epicure, Katahdin, Kennebec, Keswick, King Edward, Majestic, Saco, Sebago, South Esk, Teton and certain unnamed seedlings, including U.S.D.A. 41956 (1, 11, 12, 22).

Certain strains, including those originally designated as tuber blotch virus F (5) and pseudo-net-necrosis virus (19), produce a range of symptoms that vary according to the variety of potato and the presence of other viruses such as virus X. These strains, when introduced by sap inoculation or stem graft, induce a mild necrosis of the tips, margins and interveinal areas, especially of the lower and middle leaves. This necrosis, which frequently appears as a rustiness, is sometimes accompanied by round bright-yellow spots. In some varieties the reaction is more severe, causing a necrosis of the collenchyma of the stem and a foliar necrosis followed by a collapse of the lower and, later, the middle leaves, which may remain hanging on the stem (Figure 11). In the second and later generations the plants show bright-yellow spots and occasionally a slight rustiness of the tips and margins of the lower and middle leaves (Figure 12). The yellow spots are most pronounced when the plants are young and become less distinct as the plant matures. The tuber blotch strains generally produce typical symptoms in the following varieties: Arran Victory, Bliss Triumph, British Queen, Canso, Chippewa, Epicure, Great Scot, Irish Cobbler, Katahdin, Kennebec, Majestic, President, Russet Burbank (Netted Gem), Saco, Sebago, Teton and U.S.D.A. 41956. When some of these are introduced into varieties that are already infected with mottling strains of virus X, a diffused mottling of the interveinal areas is produced. This effect was originally described as interveinal mosaic (17) and is known to occur in the

Figures 11, 12.—Symptoms caused by virus F. 11. Necrotic symptoms in Epicure. Note necrosis of the stem and leaflets and collapse of lower leaves. 12. Yellow spotting and slight rustiness of the margins of leaflets in second-generation plants of Arran Victory.

following varieties: Arran Victory, Bliss Triumph, Early Rose, Green Mountain, Kerr's Pink, President, Russet Burbank (Netted Gem), Up-to-Date and certain unnamed seedlings. Another group of strains produce distinctive symptoms of a disease known as aucuba mosaic (13, 16, 17) (Figure 13). This disease was so named because the yellow mottling on affected leaves resembles the normal mottling on the leaves of the gold-dust tree, *Aucuba japonica* Thunb. var. *variegata* D'Ombrain. The following varieties show symptoms of aucuba mosaic when infected with the aucuba strains: Arran Victory, British Queen, Early Ohio, Epicure, Green Mountain, Irish Cobbler, President, Rural New Yorker, Russet Rural, Saco, White Rose and U.S.D.A. 41956. When some strains of virus F and virus A occur simultaneously in certain varieties, the yellow aucuba mottling is greatly intensified (5, 22). This reaction occurs in the following varieties: Arran Victory, Bliss Triumph, Golden Wonder, Green Mountain, Early Ohio, President, Russet Burbank (Netted Gem) and White Rose.

Certain virulent strains of virus F designated as virulent tuber blotch (4), Canada streak (6), Albion isolate (1), gray blotch (11, 12) and potato streak (8), when introduced by stem graft, induce a severe top necrosis followed by a necrotic streaking of the stems, petioles and larger veins. In severe cases the plants may be destroyed. The following varieties are affected in this manner: Arran Crest, Bliss Triumph, Canso, Chippewa, Epicure, Earliest of All, Irish Cobbler, Irish Daisy, Katahdin, Kennebec, King Edward, Majestic, Russet Burbank (Netted Gem), Saco, Sebago, Teton and Up-to-Date. When inoculated with sap containing

Figure 13.—Typical aucuba mosaic symptoms induced in Irish cobbler by a strain of virus F.

virus of the virulent strains, most of the varieties listed above show necrotic local lesions on the inoculated leaves and later systemic necrosis of the lower and middle leaves. The plants produced from tubers infected with the virulent strains are sometimes stunted, and show varying degrees of foliar necrosis. Chippewa and Epicure may react in this manner. A bright aucuba mosaic appears in the second and later generations of plants of the following varieties: Arran Victory, Bliss Triumph, Green Mountain, Irish Cobbler, Irish Daisy and President. When these virulent strains of virus F occur in association with virus A and virus X, the aucuba mottling is usually intensified. When they occur with virus Y there may be a rugosity and distortion of the leaves, the intensity of which varies according to the strain of each virus involved.

A distinctive feature of the F group of strains is the necrosis produced in the tubers of certain varieties. This symptom was first called pseudo-net-necrosis (19) and later tuber blotch (5). The necrosis consists of blotches in the pith and cortex, usually originates at the stem end and often extends throughout the interior of the tuber (Figure 14). Sometimes the lesions occur externally as irregular, sunken necrotic areas, which may involve and destroy the eyes. This tuber necrosis usually develops after the tubers are 2 to 3 months in storage and it is accelerated by a rise in temperature. The following varieties show necrotic symptoms in the

Figure 14.—Katahdin tubers showing symptoms produced by a strain of virus F. Note necrotic blotches in the interior and depressed necrotic lesions on the surface.

tubers when infected with the tuber blotch strains: Arran Victory, Bliss Triumph, Chippewa, Green Mountain, Irish Cobbler, Katahdin, Kennebec, King Edward, Majestic, President, Russet Burbank (Netted Gem), Saco, Sebago, Up-to-Date and U.S.D.A. 41956. The aucuba strains produce necrotic symptoms in the tubers of the following varieties: British Queen, Great Scot, Majestic and President.

It is noteworthy that the insect *Phenacoccus aceris* (Signoret) produces round, bright-yellow spots on the lower and middle leaves of potatoes closely resembling the aucuba mosaic symptoms induced by strains of virus F. The insect colonizes on apple trees and disperses from this host to potatoes.

RESISTANT AND IMMUNE SOURCES

An interspecific potato hybrid, *Solanum tuberosum* var. Epicure × 4n *S. chacoense,* is highly resistant to virus F. This seedling developed a form of foliar and top necrosis when each of 6 isolates of virus F were introduced by stem graft (1). *Solanum capsicastrum* Link appears to be immune to most strains of virus F (1).

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VIRUS M

SYNONYMS

Leafrolling mosaic, Schultz & Folsom; interveinal mosaic, Schultz; paracrinkle virus, Salaman & LePelley; potato virus E, Bawden; potato virus E, Dykstra; potato virus K, Köhler; potato virus 7, J. Johnson; *Solanum virus* 7, Smith; *Solanum virus* 11, Smith; *Marmor angliae,* Holmes; potato virus M, Bagnall, Larsen & Walker.

This virus was only recently separated from various complexes that included virus S and virus X. It is now distinguished as a separate virus (1, 3).

HOST RANGE

AMARANTHACEAE: *Gomphrena globosa* L.; LEGUMINOSAE: *Cyamopsis tetragonoloba* (L.) Taub., *Vigna sinensis* Endl.; SOLANACEAE: *Browallia elata* L., *Datura bernhardii* Lund., *D. metel* L., *D. ecklonis* L., *D. stramonium* L., *D. stramonium* var. *tatula* (L.) Torr., *Lycopersicum esculentum* Mill., *Nicotiana debneyi* Domin., *Physalis pubescens* L., *Saracha umbellata* Don., *Solanum demissum* Lindl., *S. melongena* L., *S. rostratum* Dunal., *S. sisymbriifolium* Lam., *S. tuberosum* L., *S. villosum* Lam.

TRANSMISSION

The virus is transmitted by stem graft and by sap inoculation to potato and certain solanaceous and nonsolanaceous plants (1, 4, 15, 16).

All the known strains, including the one inducing paracrinkle[1], are transmitted by the aphid *Myzus persicae* (Sulz.) (8, 9, 15, 19, 21). The leafrolling mosaic strain is transmitted also by *Macrosiphum euphorbiae* (Thom.) and *Myzus perlargonii* (Kltb.) (19) (=*Acyrthosiphon malvae* (Mosley) *partim*).

PHYSICAL PROPERTIES

Most strains are inactivated by heating from 65° to 70°C. for 10 minutes. The dilution end point ranges from 1:40 to 1:100 and the longevity in vitro varies from 2 to 4 days at 20° to 22°C. The virus was maintained over anhydrous calcium chloride at 5°C. for 11 months (1, 4). The particles are rigid to slightly flexible rods 651 mμ long and 12 to 13 mμ wide (5, 6, 15, 20).

IMMUNOLOGICAL AND SEROLOGICAL RELATIONSHIPS

Within the M group of strains there is strong mutual interference but there is apparently no protection effected by strains of virus M against strains of the related virus S (15). Weak strains of virus M protect plants against the more virulent forms (15).

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[1]Kassanis, B. Potato paracrinkle virus. Eur. Potato J. 4:13-24. 1961.

Virus M is strongly antigenic and a high-titer antiserum has been prepared from clarified sap and purified suspensions of the virus. This antiserum is effective for the detection of the virus in the sap of potatoes and other solanaceous and nonsolanaceous plants (1-3, 14, 15).

Since virus M and virus S are serologically related and have certain features in common they may have had a common ancestry (1, 3).

INDICATOR HOSTS

When introduced by sap inoculation, virus M produces distinctive and diagnostic symptoms in the following plants (1, 3, 15):

Datura metel. Diffused chlorotic to necrotic local lesions appear in 8 to 14 days. Later, similar systemic lesions are produced (Figure 15).

Nicotiana debneyi. Irregular, brown ringlike local lesions are induced in 10 to 14 days. The virus does not become systemic in this plant (Figure 16).

Solanum rostratum. Systemic symptoms, including necrotic streaking of the stems, petioles and main leaf veins, appear in 30 to 40 days.

Vigna sinensis. Irregular, reddish necrotic local lesions appear in 12 to 14 days in certain clones.

The virus does not produce symptoms in *Browallia elata, Lycopersicum esculentum, Physalis pubescens, Solanum melongena, S. sisymbriifolium* and *S. villosum* (1, 4, 10, 15).

Virus M may be distinguished from the related virus S by the local and systemic symptoms produced by the former in *Datura metel* (3). Virus S produces only faint transient symptoms in this plant. In *Solanum rostratum,* virus M also produces distinctive symptoms, necrotic streaking of the stem, petioles and major veins of the leaves, whereas virus S induces irregular necrotic systemic lesions (3). The following hosts accept virus M and exclude virus S when introduced in a mixture: *Lycopersicum esculentum, Solanum melongena* and the potato variety Saco (3).

When virus M and virus S are present together in the sap of certain potatoes such as U.S.D.A. 41956, virus S can be eliminated by heating the mixture at 65°C. for 10 minutes.

SYMPTOMS INDUCED IN POTATO

Virus M occurs in strains, the symptoms of which vary according to the variety infected (1, 15). A strain of this virus has been established (1, 3) as a component of interveinal mosaic (17) and leafrolling mosaic (18). In these diseases virus M occurs in association with virus S and virus X. It has not been determined if all three viruses must be present to produce the symptoms attributed to the two diseases in affected varieties.

Interveinal mosaic is distinguished by a diffuse interveinal mottling and no deformation or rolling of the leaves (Figure 17). The mottling is intensified by cool cloudy conditions and becomes indistinct when the temperature is 24° C. or higher. Some clones of British Queen, Epicure, Irish Cobbler, Katahdin, Pontiac, Sebago, Warba and Up-to-Date may show symptoms of interveinal mosaic when infected with the M-S-X virus complex.

Figures 15, 16.—Symptoms caused by virus M. 15. Left, diffused chlorotic and necrotic lesions in *Datura metel;* right, normal plant (R. H. Bagnall). 16. Irregular, ring-like local lesions in *Nicotiana debneyi* (R. H. Bagnall).

Figure 17.—Diffuse interveinal mottling caused in Green Mountain by a strain of virus M. (R. H. Bagnall)

The distinctive features of leafrolling mosaic are an upward rolling and flaccidity of the leaves, a diffuse interveinal mottling and some stunting of the plant (Figure 18). The rolling and mottling may become indistinct and may disappear when the temperature rises above 24° C. In some cases the main veins and petioles show brownish necrotic streaks. The symptoms in later generations are similar to, but more intense than, those described for the first season. There are no tuber symptoms. The M-S-X virus complex produces symptoms of leafrolling mosaic in the following varieties: Bliss Triumph, Early Rose, Early Ohio, Green Mountain, President and White Rose. The M strain that is associated with leafrolling moasic may also be a component of the disease known as curly dwarf, which has been described as occurring in Green Mountain, Russet Rural, Rural New Yorker (Dooley) and other varieties (18).

A source of virus M designated as the paracrinkle strain has been identified in the King Edward variety (1). This strain produces a slight ruffling and paling of the leaves in King Edward and possibly other varieties. When King Edward scions bearing this strain of virus M are grafted to Arran Victory the distinctive disease paracrinkle (1, 16) is produced. The first symptoms are a clearing of the

Figure 18.—Leafrolling mosaic caused in Green Mountain by a strain of virus M. (R. H. Bagnall)

veins and the development of bright chlorotic blotches at the junctions of the larger veins and the main vein and a puckering of the leaf blade and waviness of its margins (Figure 19). These chlorotic areas become larger and the leaves become severely deformed and reduced in size. Sometimes there are irregular necrotic lesions in the interveinal spaces and intermittent brownish streaks on the veins, petioles and stems. In subsequent generations the affected plants are severely stunted and brittle, the leaves being grossly deformed and clumped together to give a curly dwarf effect (Figure 20). The paracrinkle virus complex produces a mild crinkle mosaic in Arran Comrade, Great Scot and Majestic, and mosaic-like blotches with no rolling or crinkling in Bliss Triumph, Green Mountain, Russet Burbank (Netted Gem), Spaulding Rose and White Rose (7).

Three strains of virus M have also been differentiated in the Netherlands (15). The one designated as M-Bi, obtained from the Bintje variety, does not produce symptoms in clones of Green Mountain, Irish Cobbler, Sebago, U.S.D.A. 41956 or certain European varieties. This strain produces a mild interveinal mottling

Figures 19, 20.—Symptoms caused by virus M in Arran Victory. 19. Early symptoms (bright chloritic blotches and vein clearing). 20. Curly dwarf effect.

and slight deformation of the leaves in such varieties as Arran Victory, Bintje, Katahdin, Fortuna, Kennebec and White Rose. It produces much stronger mosaic symptoms and deformation of the leaves, and a slight necrosis of the leaf petioles and stems, in such varieties as Eigenheimer, Majestic, Saco and Voran. The strain named M-Fort, obtained from the Fortuna variety, is more virulent than M-Bi and produces severe symptoms, mottling, deformation and bronzing of the leaves, in certain varieties, including Bintje, Green Mountain, Irish Cobbler and U.S.D.A. 41956. When infected with the M-Fort strain, some varieties such as Eigenheimer and Frisco develop a severe necrosis on the leaf petioles and veins, severe crinkling of the leaves and a stunting of the plant. A strain called M-U.D., obtained from a healthy plant of the Up-to-Date variety, is more virulent than the M-Bi, M-Fort and paracrinkle strains. In the Bevelander and Prinslander varieties it produces a severe mottling and crinkling of the leaves, necrosis of the petioles and main veins, and a blue discoloration of the tips of the leaflets.

Virus M has been reported as occurring naturally in several varieties in the United States (1, 11, 17), in France (14) and in Germany (8). It also occurs in certain varieties in Canada (1, 12, 13), including Bliss Triumph, Green Mountain and Irish Cobbler. The King Edward variety, originated in England, is believed to be universally infected with the paracrinkle strain (16, 19).

RESISTANT AND IMMUNE SOURCES

Most of the potato varieties that are immune to virus A and virus X are susceptible to virus M (17). The following solanaceous plants are apparently immune to virus M: *Capsicum annuum, Nicandra physalodes, Nicotiana glutinosa, N. sylvestris, N. tabacum* and *Physalis floridana* (1, 3, 10, 15). No tuber-bearing solanums have been reported as resistant or immune to virus M.

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VIRUS S

HOST RANGE

AMARANTHACEAE: *Gomphrena globosa* L.; CHENOPODIACEAE: *Chenopodium album* L.; LEGUMINOSAE: *Cyamopsis tetragonoloba* (L.) Taub., *Vigna sinensis* Endl.; SOLANACEAE: *Browallia elata* L., *Datura bernhardii* Lund., *D. ecklonis* L., *D. metel* L., *D. stramonium* L., *D. stramonium* var. *tatula* (L.) Torr., *Nicotiana debneyi* Domin., *Physalis philadelphica* Lam., *P. pubescens* L., *Saracha umbellata* Don., *Solanum acaule* Bitt., *S. andigenum* Juz. & Buk., *S. brevimucronatum* Hawk., *S. caldasii* Dun., *S. chacoense* Bitt, *S. commersonii* Dun., *S. demissum* Lindl., *S. goniocalyx* Juz. & Buk., *S. longipedicellatum* Bitt., *S. malinchense* Hawk., *S. pinnatisectum* Dun., *S. polyadenium* Greenm., *S. rostratum* Dun., *S. rybinii* Juz. & Buk., *S. sisymbriifolium* Lam., *S. stoloniferum* Schlechtd., *S. tuberosum* L., *S. villosum* Lam.

TRANSMISSION

The virus is transmitted to potato by stem graft, by tuber plug graft, by sap inoculation and by direct contact of diseased and noninfected plants (12, 20, 21, 23). It is also transmissible by sap inoculation to certain solanaceous and nonsolanaceous hosts (4, 5, 30).

PHYSICAL PROPERTIES

The virus is inactivated by heating at 55° to 60° C. for 10 minutes (4, 23). The dilution end point is 1:1,000 and the longevity in vitro varies from 3 to 6 days at 20° to 22° C. (4, 13, 23). Virus S remained viable for 11 months when maintained over anhydrous calcium chloride at 5° C. (4). The particles are flexible threads 657 mμ long and 12 to 13 mμ wide (7, 11).

IMMUNOLOGICAL AND SEROLOGICAL RELATIONSHIPS

This virus was first detected by serology during an attempt to prepare an antiserum against virus A by using the variety Light Industry as a source of material (9, 26). It was named virus S after Prof. E. Van Slogteren, who directed the work that led to its discovery at the Laboratory for Flower-bulb Research at Lisse, Netherlands. The virus is strongly antigenic and an antiserum of high titer has been produced and used effectively in detecting this virus in several varieties of potatoes and certain other solanaceous hosts (3-5, 14, 26).

Mild and severe strains of virus S have been reported (2, 4, 17, 23). Preliminary tests have shown that one strain protects against the others (23). Two viruses now designated as carnation latent (13) and virus M (4) are serologically related to virus S and may have originated from a common ancestor (5).

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INDICATOR HOSTS

Virus S produces distinctive symptoms in the following plants (4, 5):

Nicotiana debneyi. About 20 days after inoculation by sap a vein clearing appears on the first leaf above the basal whorl and spreads from the tip toward the base of the leaf. Later the higher leaves develop, in succession, a similar vein clearing, which is eventually replaced by a vein banding and interveinal mottling (Figure 21). Finally the affected leaves become chlorotic and develop necrotic lesions in the interveinal areas. The serologically related virus M produces local lesions but no systemic symptoms in this host.

Figure 21.—Left, normal leaf of *Nicotiana debneyi.* Right, vein clearing caused in *N. debneyi* by virus S. (R. H. Bagnall)

Solanum villosum. Several weeks after inoculation the virus incites systemic chlorotic leaf blotches, which sometimes assume a ring-shaped appearance.

Solanum rostratum. Within 20 days after inoculation the virus incites irregular, dark necrotic lesions on the inoculated leaves. Later, similar lesions appear on the higher leaves. The affected plants are usually stunted but the petioles and stems remain normal and there is no interruption of apical development.

Chenopodium album. In 20 days the virus produces small yellow lesions on the inoculated leaves. Later these lesions are surrounded by dark-green rings on the matured chlorotic leaves. The related virus M is usually symptomless in this host.

Cyamopsis tetragonoloba. From 6 to 12 days after inoculation, small brown necrotic local lesions appear on the cotyledons.

Datura metel. The virus becomes systemic but usually does not produce symptoms. Occasionally there is a faint, transient mottling.

Virus S does not produce symptoms in *Browallia elata, Physalis pubescens, Solanum sisymbriifolium, S. villosum* or *Vigna sinensis.*

SYMPTOMS INDUCED IN POTATO

The symptoms in potato vary according to the variety, and possibly the strain (8, 23, 27). In some varieties the virus produces only a mild mottling, which is more pronounced under cool, cloudy conditions but usually not discernible when normal weather prevails (22). The fugitive so-called weather mottle, which appears occasionally in certain commercial varieties, may be due in part to this virus. The following varieties sometimes react in this manner: Arran Victory, Bliss Triumph, Chippewa, Epicure, Green Mountain, Irish Cobbler, Katahdin, Kennebec, King Edward, Warba and White Rose.

The following varieties show a slight stunting, light-green color (sometimes a paleness), faint interveinal mottling and a mild rugosity of the foliage: Eigenheimer, President, Sebago and Up-to-Date.

A group of varieties and seedlings show a definite alteration of growth habit, distinct interveinal mottling, slight vein banding, downward rolling and severe rugosity of the leaves and, especially in older plants, a weakening of the stems that produces a drooping effect.

Other varieties manifest a definite stunting, open growth, interveinal mottling, and distinct deepening of the veins that makes the leaves seem to be rugose. Sometimes the lowest leaves are pale and flaccid. Arran Banner, Bintje, Majestic, Voran and other European varieties behave in this manner.

In still other varieties there is also a marked bronzing, and fine dark necrotic lesions develop on the upper surfaces of the apical leaves. In addition, the leaves of some of these varieties, when maturing, develop greenish-yellow or greenish-bronze spots over the entire surface. These spots have a high accumulation of starch, which can be demonstrated by the standard iodine test. These symptoms are distinctive and may be used for the diagnosis of this virus in the following varieties: Bevelander, Fortuna, Glorea and Profijt (23).

Noteworthy in certain varieties is the similarity between the symptoms produced by virus S and those associated with potash deficiency, especially the bronzing, downward rolling, rugosity, and the fine necrotic spotting of the leaves (28). To avoid confusion, this similarity in symptoms should be taken into consideration when determining the presence of virus S and evaluating the effects of potash deficiency.

In general, virus S reduces the yield and the number of tubers. In addition, plants with extreme symptoms such as rugosity and crinkling are more subject to wind injury than noninfected plants with smoother surfaces. Because flower production is reduced in plants infected with virus S, stocks intended for breeding purposes should be maintained free from this virus.

Virus S in combination with virus A, X or Y apparently does not produce synergism. There is, however, some intensification of such symptoms as mottling and rugosity, dependent on the variety involved, especially when virus S is present with virus A and virus Y. In general, the symptoms of virus S appear later than those of virus A and virus Y (23).

Virus S is widespread in several commercial varieties in Europe (8, 16, 19, 20, 23, 24, 29), North America (3, 5, 10 23, 27) and New Zealand (25). Clones of the following varieties registered in Canada have been found naturally infected: Arran Victory, Bliss Triumph, Canso, Chippewa, Epicure, Green Mountain, Irish Cobbler, Katahdin, Kennebec, Keswick, King Edward, Majestic, Russet Burbank (Netted Gem), President, Russet Rural, Warba and White Rose (2, 3, 27).

Plants of King Edward variety apparently free from virus S have been produced by growing a portion of the apical meristem on agar culture, then grafting this shoot onto *Lycopersicum esculentum* and making a cutting of the grafted shoot (15).

RESISTANT AND IMMUNE SOURCES

The Saco variety is considered highly resistant or immune to virus S (1, 4). This virus, however, when introduced to Saco by top-graft inoculation can pass through the stem tissue into the roots, from which it may be recovered (18). The resistance of Saco to virus S appears to be derived in part from one of its parents, the virus-X-immune U.S.D.A. 41956. But in seedling populations, resistance to viruses S and X has segregated independently (6). The following solanaceous plants appear to be immune to virus S: *Capsicum annuum, Datura stramonium, Lycopersicum esculentum, Nicotiana tabacum, N. glutinosa,* N. *sylvestris, Nicandra physalodes, Physalis floridana and Solanum melongena* (5, 19).

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VIRUS X

SYNONYMS

Potato mottle virus, J. Johnson; potato latent virus, Schultz; potato healthy virus, E. M. Johnson; potato simple mosaic, Murphy; potato virus 16, J. Johnson; *Solanum virus* 1, Smith; *Marmor dubium* var. *vulgare,* Holmes; *Solanumvirus annulosum,* Köhler; *Minflexus solani,* Hansen.

HOST RANGE

AMARANTHACEAE: *Amaranthus caudatus* L., *A. hybridus* L., *A. retroflexus* L., *A. tricolor* L., *Gomphrena globosa* L., *Iresine herbstii* Hook.; CHENOPODIACEAE: *Beta vulgaris* L., *Chenopodium album* L., *C. amaranticolor* Coste & Reyn., *C. quinoa* L., CONVOLVULACEAE: *Cuscuta campestris* Yuncker; LABIATAE: *Lamium hybridum* Vill., *L. purpureum* L., *Nepeta cataria* L., *Ocimum basilicum* L., *Salvia lancaefolia* Poir., *Satureai hortensis* L.; LEGUMINOSAE: *Trifolium incarnatum* L.; *T. pratense* L.; RUTACEAE: *Citrus aurantium* L. var. *sinensis* L., *C. limonia* Osbeck.; SCROPHULARIACEAE: *Digitalis lanata* Ehrh., *D. ambigua* Murr., *Linaria bipartita* Willd., *L. cymbalaria* (L.) Mill., *L. maroccana* Hook., *L. vulgaris* Hill., *Veronica agrestis* L., *V. longifolia* L., *V. orchidea* Crantz., *V. serpyllifolia* L., *V. teucrium* L.; SOLANACEAE: *Atropa, Browallia, Capsicum, Chamaesaracha, Cyphomandra, Datura, Hyoscyamus, Lycopersicum, Lycium, Nicandra, Nicotiana, Petunia, Physalis, Salpiglossis, Scopolia, Schizanthus* and *Solanum,* including *S. acaule* Bitt., *S. ajuscoense* Buk., *S. americanum* Mill., *S. andigenum* Juz & Buk., *S. antipoviczii* Buk., *S. appendiculatum* Humb. & Bonpl., *S. bulbocastanum* Dun., *S. capsicastrum* Link, *S. cardiophyllum* Lind., *S. carolinense* L., *S. chaucha* Juz. & Buk., *S. citrullifolium* A. Br., *S. demissum* Lindl., *S. dulcamara* L., *S. fendleri* Gray, *S. goniocalyx* Juz. & Buk., *S. insulatum* L., *S. integrifolium* Poir., *S. jamesii* Torr., *S. jasminoides* Paxt., *S. melongena* L., *S. miniatum* Bernh., *S. multidissectum* Hawkes, *S. muricatum* Ait., *S. neoantipoviczii* Buk., *S. nigrum* L., *S. nigrum* var. *nodiflorum* L., *S. phureja* Juz. & Buk., *S. pinnatisectum* Dun., *S. polyadenium* Greenm., *S. pseudocapsicum* L., *S. racemigerum* L., *S. roberti-eliae* L., *S. rostratum* Dun., *S. rubrum* L., *S. schenkii* Bitt., *S. schickii* Juz. & Buk., *S. sisymbriifolium* Lam., *S. sodomaeum* L., *S. stenotomum* Juz & Buk., *S. stoloniferum* Schlechtd., *S. trifidum* Correll., *S. tuberosum* L., *S. verrucosum* Schlechtd., and *S. yabari* Hawkes.

TRANSMISSION

The virus is easily transmitted by sap inoculation, by stem and tuber graft, by the dodder *Cuscuta campestris* (17) and by the grasshopper *Melanoplus differentialis* (Thos.) (32). It is spread in the field by contact between healthy and infected plants (18) and underground by root contact (23). It can also

be spread by the cutting knife (20), by sprout contact (6) and by the implements used in field operations. As the virus can persist up to six weeks on the clothing of human beings and the fur of such animals as dogs and rabbits, it can be spread by these agencies within the crop and from one crop to another (30). Virulent strains, which are more highly concentrated in infected plants, spread more readily than avirulent forms (9).

PHYSICAL PROPERTIES

These properties vary with the strain involved. Most strains are inactivated by heating at 68° to 70° C. for 10 minutes. The dilution end point ranges from 1:100,000 to 1:1,000,000 and resistance to aging varies from 1 to several months at 20° to 22° C. (17, 24, 28). In electron-microscopic observations (8) the particles of the virus are flexible threads 515 mμ long and 10 or 11 mμ wide. But in flow birefringence studies (22) it was found that the virus behaves like a rigid particle and is from 540 to 620 mμ long. Intracellular inclusions (X bodies) are often present in potato plants infected by virus X. They occur more abundantly in potatoes that show a mottle symptom or carry the virus without symptoms and are more common in the palisade cells and in the spongy parenchyma. These X bodies vary in diameter from 6 to 50 μ (11).

IMMUNOLOGICAL AND SEROLOGICAL RELATIONSHIPS

When susceptible varieties of *Solanum tuberosum, Nicotiana tabacum* var. White Burley, *Datura stramonium* and certain other solanaceous hosts are systemically infected with a weak mottling strain of virus X, such plants are protected against invasion by virulent strains (24, 31). The various strains of virus X are all mutually protective (28). If weak and virulent strains are introduced simultaneously and in equal amounts, infection by both types of strains is possible. Weak and virulent forms of virus X have been found together in potatoes under natural conditions (17, 19, 24). Many clones of the following commercial varieties registered in Canada harbor a mottle strain and the B strain of virus X: Bliss Triumph, Early Ohio, Green Mountain, Irish Cobbler, McIntyre, Russet Burbank (Netted Gem) and White Rose. Weak mottling and virulent (ringspot) strains were found together in certain varieties, including Bliss Triumph, Chippewa, Early Rose, Green Mountain, Irish Cobbler, Katahdin, Pontiac, Rural New Yorker (Dooley), Russet Rural, Spaulding Rose, Warba and White Rose (17, 19).

Virus X is strongly antigenic. A highly satisfactory antiserum prepared against this virus has been made from clarified sap and purified suspensions of the virus from infected *Nicotiana tabacum, Datura stramonium* and other solanaceous hosts (4, 6, 10). When kept sterile at 1° C. this antiserum retains a high precipitin titer for several years. The precipitin reaction can be used for detecting the virus in the sap of susceptible varieties of *Solanum tuberosum* and other solanceous plants (4, 31). The complement fixation reaction (4) is more sensitive than that of the precipitin test but as the complement fixation test is rather complicated it is not used extensively for determining the presence of virus X.

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INDICATOR HOSTS

On *Gomphrena globosa* all the known strains of virus X produce distinctive local lesions that have a white spot encircled by a dark-red ring (33) (Figure 22).

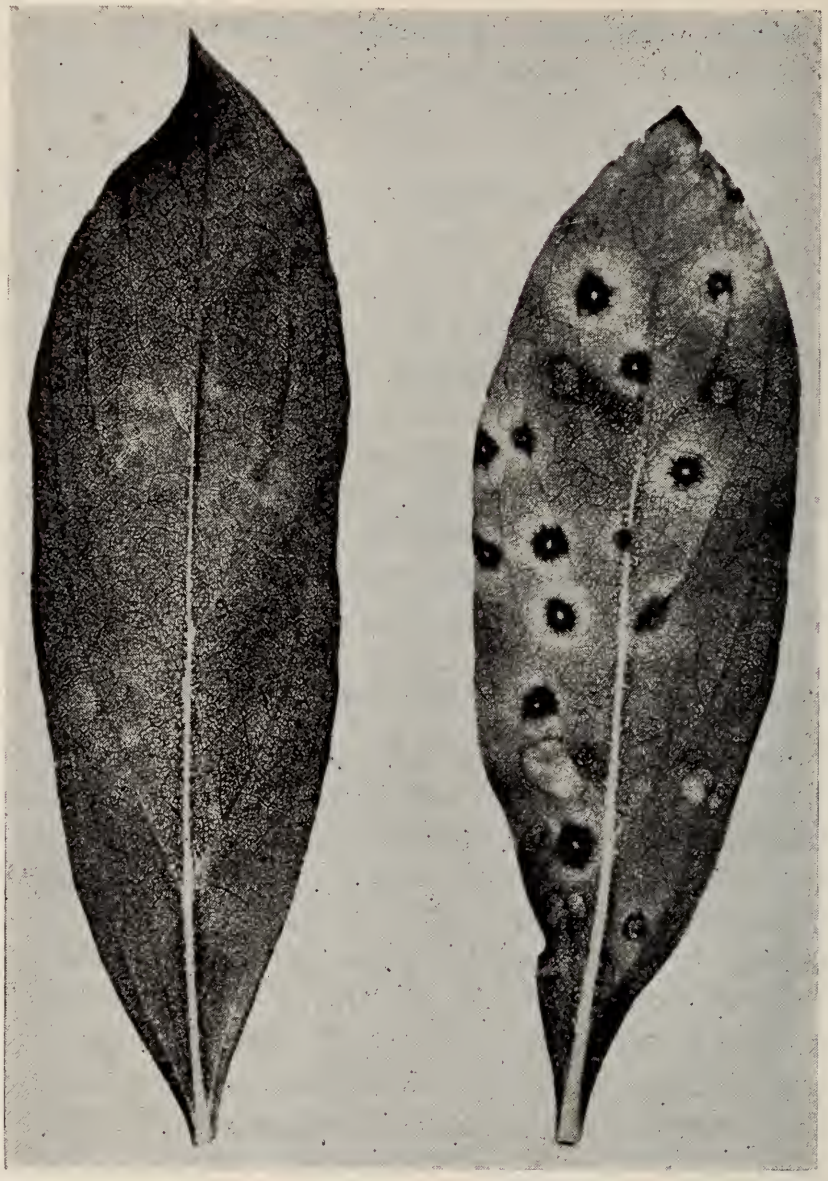


Figure 22.—Local lesions produced in *Gomphrena globosa* by virus X. Note dark (red) rings with white centers. (R. H. Bagnall)

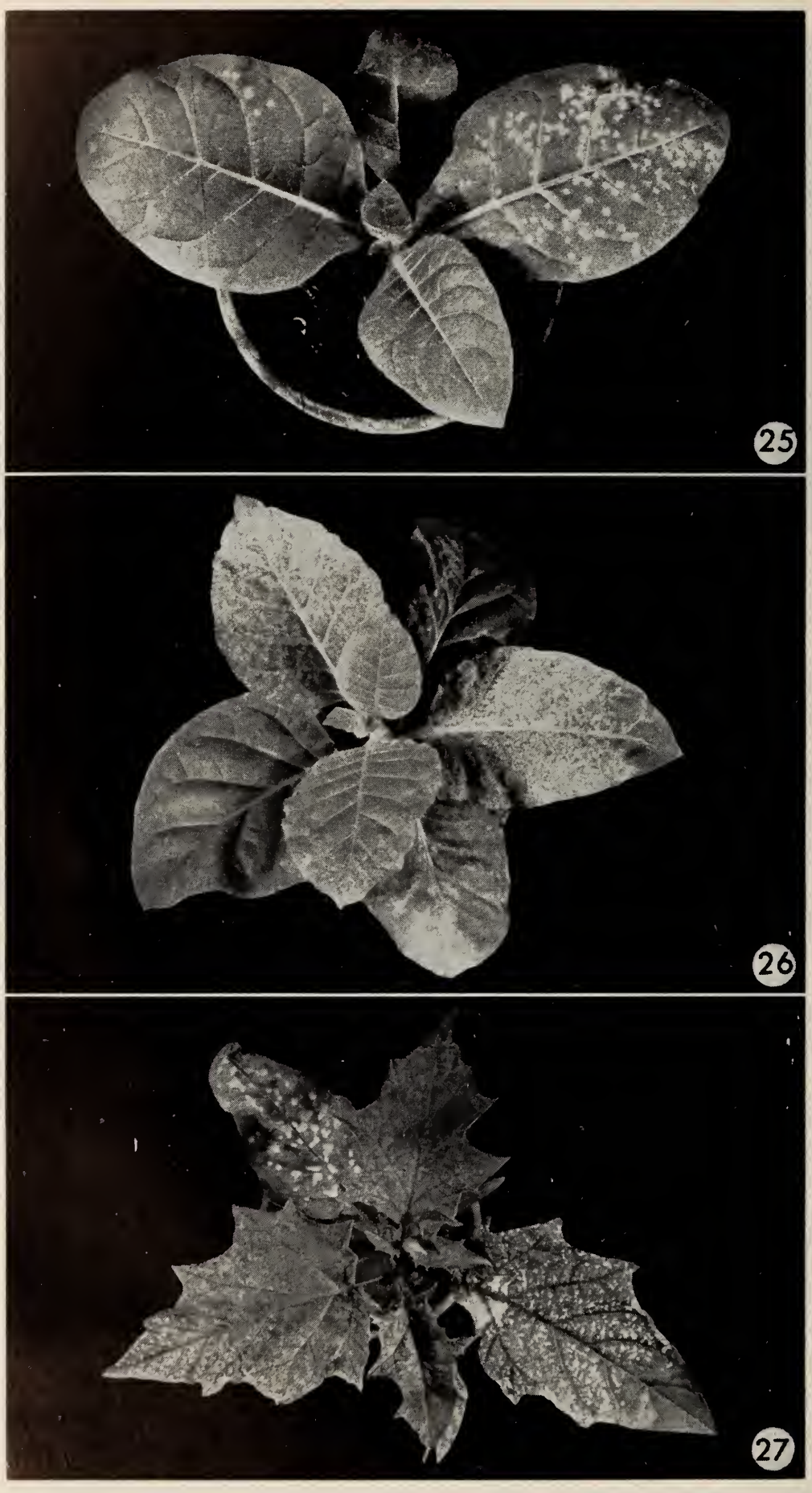
The local lesions are more clearly defined when the plant is inoculated before it flowers. *Chenopodium amaranticolor* shows similar symptoms. *Datura stramonium* and *D. stramonium* var. *tatula* and *Nicotiana tabacum* (White Burley and Samsun) are useful indicators for virus X. In these hosts there is a vein clearing, mottling, ring spot, local lesions, and systemic necrosis, according to the strain concerned (Figures 23-27). The mildest strains usually produce no symptoms in these hosts. All the common strains of virus X produce in *Capsicum annuum* necrotic local lesions followed by a severe systemic necrosis of the leaves and stem. *Nicotiana rustica* is also a suitable host for virus X because it distinguishes the groups of strains that produce mottle, necrotic or yellow symptoms.

Figures 23, 24.—Symptoms caused by virus X in *Nicotiana tabacum* (White Burley). 23. Early symptom (vein clearing). 24. Mottling and vein banding produced by a medium strain of the virus.

When virus X is introduced simultaneously with virus Y into White Burley and Samsun varieties of *N. tabacum,* the symptoms normally induced by these viruses are greatly intensified. The veins first assume a brighter yellow color and later become necrotic; subsequently the leaves develop a severe mottling and systemic necrosis, which may cause collapse of the leaves (Figure 28). The intensity of this reaction depends on the virulence of the strains of the combining viruses. An abnormal graft reaction takes place when scions bearing virus X are grafted on immune stocks such as U.S.D.A. 41956 (21). Aerial tubers are formed on the scions, and the underground portions of the stalks develop a severe necrosis. This reaction is useful for showing the presence of virus X and determining immunity to this virus in potatoes. A genetical basis for the classification and separation of strains of virus X has been outlined (14). This scheme distinguishes four groups of strains of the virus by the use of a number of potato varieties, the distinction being made by the presence or absence of the two genes (Nx and Nb, each inherited independently) that control hypersensitivity.

SYMPTOMS INDUCED IN POTATO

This virus occurs in a number of strains (1, 2, 12, 15-17, 19, 24, 28, 29), the symptoms varying according to the potato variety and the strain involved. Certain strains produce faint or nonvisible symptoms in a number of commercial varieties, including Bliss Triumph, Chippewa, Early Rose, Green Mountain, Irish Cobbler, Katahdin, Keswick, Russet Burbank (Netted Gem), Pontiac, Sebago, Warba and White Rose. Most stocks of these varieties are universally infected by one or more strains of virus X. Other strains produce in the same varieties a simple interveinal mottling and no deformation of the leaves or dwarfing of the plant (Figure 29). More virulent strains induce in these varieties a severe mottling, interveinal

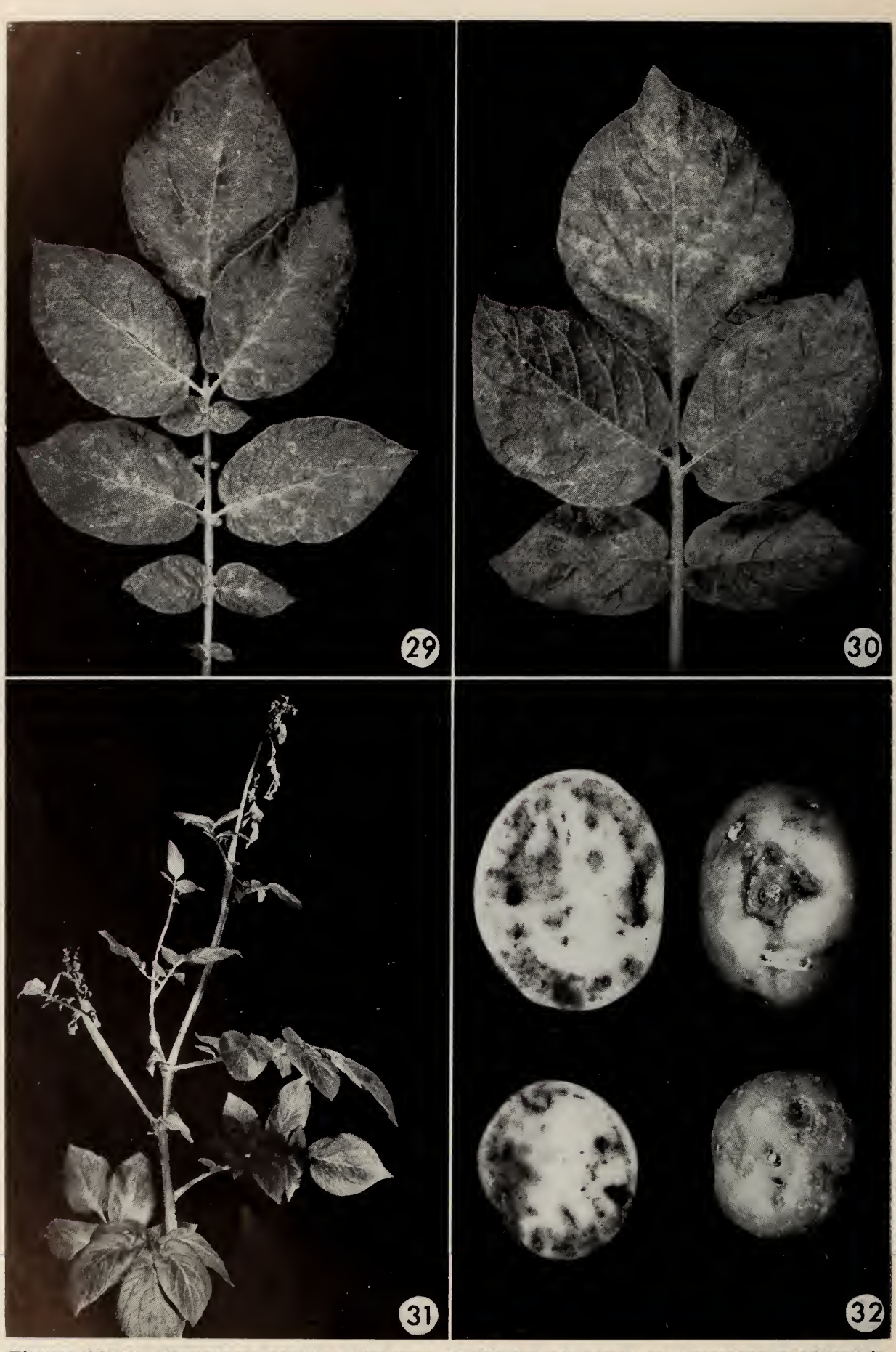


Figures 25-27.—Symptoms produced by a virulent strain of virus X. 25. Necrotic local lesions in *Nicotiana tabacum* (White Burley). 26. Systemic necrosis and ring spotting in *N. tabacum* (White Burley). 27. Local lesions and systemic necrosis in *Datura stramonium*.

Figure 28.—Synergistic effect in *Nicotiana tabacum* (Samsun) when common strains of virus X interact with strains of virus Y.

necroses, unevenness of the leaf blade (Figure 30) and stunting of the plant. When certain varieties are infected by virus X a top necrosis similar to that produced by virus A is observed (3). This acute necrosis generally destroys the growing point and the top leaves (Figure 31) and eventually most of the stems, the lower leaves and the tubers. The infected tubers develop a severe necrosis of the surface and the interior (Figure 32) and many so affected are destroyed. When infected tubers germinate they usually give rise to dwarfed necrotic plants, which soon wilt and die. This extreme susceptibility, known as hypersensitiveness, constitutes a form of immunity, and potatoes that react in this manner rarely become infected by virus X in the field. The following varieties are hypersensitive or field-immune to virus X: British Queen, Craig's Defiance, Epicure, Hunter, King Edward and certain unnamed seedlings of American and Canadian origin.

A strain designated as B (3, 5, 24, 28) produces faint mottling or no symptoms in certain varieties, including Ashworth, Bliss Triumph, Canoga, Cayuga, Chisago, Delus, Early Ohio, Early Rose Fillmore, Green Mountain, Houma, Irish Cobbler, Kasota, Kennebec, La Soda, Mesaba, Mohawk, Russet Burbank (Netted Gem), Ontario, Pawnee, Potomac Red McClure, Rural New Yorker, Russet Rural, Saranac, Spaulding Rose, Up-to-Date, Warba and White Rose. Strain



Figures 29-32.—Symptoms produced by virus X. 29. Simple interveinal mottling produced in Green Mountain by a medium strain of the virus. 30. Severe mottling and unevenness of the blade produced in Green Mountain by a virulent strain. 31. Top necrosis in Epicure. 32. Internal and external necrosis in Epicure tubers.

B occurs naturally in some of these varieties, especially the older ones. This strain differs from the ordinary ones in that it causes a top necrosis and a necrosis of the tubers in certain varieties not so affected by other strains. The varieties are: Arran Victory, Avon, British Queen, Canus, Canso, Cherokee, Chippewa, Desota, Fundy, Essex, Huron, Katahdin, Keswick, La Salle, McIntyre, Menominee, Norkota, Pontiac, Pungo, Redkote, Satapa, Sebago, Seneca, Sequoia, Teton and Yampa. Being hypersensitive to strain B, these varieties are rarely attacked by it in the field. A strain somewhat similar to B, found in Green Mountain (14), produces top necrosis in King Edward but not in Epicure and Katahdin.

Another strain designated as D (2) produces a distinctive foliar necrosis in certain varieties, including Arran Victory, British Queen, Chippewa, Katahdin, Kerr's Pink, Pontiac and some unnamed seedlings. When the virus is transmitted by sap inoculation, circular brownish-black necrotic local lesions, which penetrate to the lower surface of the leaf, are produced. Later, systemic symptoms appear as necrotic blotches on the leaves that occupy the lower and intermediate positions on the stem (Figure 33). These necrotic areas enlarge and coalesce, and cause

Figure 33.—Circular necrotic lesions produced in a potato seedling by the D strain of virus X.

the leaves to collapse and fall off. As the plant matures, the wilting and leaf drop cease and the new leaves at the top of the plant show a blotchy interveinal mottling, small scattered necrotic lesions, and a crinkling of the surface. In succeeding generations the infected plants may show only the interveinal mottling, slight necrotic spotting and some deformity of the leaves. In Epicure and King Edward, strain D causes a top and tuber necrosis similar to that induced by the ordinary strains.

The virulent strains designated as N (24), ringspot (17) and severe (12) produce severe necrotic symptoms and mottling in varieties such as Arran Victory, Canso, Chippewa, Keswick, Katahdin, Kennebec, Pontiac, Sebago and Sequoia. Bliss Triumph, Green Mountain, Irish Cobbler, Early Rose, White Rose and certain other old varieties are rarely attacked by these strains in the field because most stocks of these potatoes are already infected by weak strains of virus X, which protect against entry of the virulent forms. When these virulent strains are introduced to susceptible varieties by sap inoculation, circular necrotic local lesions develop on the inoculated leaves. This symptom is followed by an interveinal necrosis and crinkling of the leaves in the lower and middle sections of the plant. Later the leaves in the top section show an interveinal mottling, scattered necrotic flecking and moderate crinkling. In some cases the larger veins, petioles and stems of the affected plants develop severe necrotic streaks. As the plant grows older the lower and middle leaves become increasingly necrotic, collapse and fall off (Figures 34, 35). In severe cases the plants are destroyed before tubers are formed. The tubers produced on infected plants show no symptoms but they give rise to weak plants that have necrotic symptoms similar to those induced during the period of primary infection. In succeeding generations the infected plants seem to become tolerant of the virus and show mild necrotic symptoms, less crinkling and a milder mottling. These severe strains also produce a typical top necrosis in Epicure, King Edward and other varieties that react in this manner to the ordinary strains. The symptoms produced by some of these necrotic strains resemble the mild, crinkle and rugose mosaic diseases caused when virus X occurs in combination with virus A or virus Y in such varieties as Bliss Triumph, Early Rose, Green Mountain, Keswick and White Rose. The symptoms produced by the virulent strains of virus X may be distinguished from those of the A and X and the X and Y virus complexes by the necrotic lesions produced on the leaves and the irregular mottling associated with the virulent strains when acting alone. In the rugose mosaic disease (viruses X and Y) there is a more pronounced crinkling (rugosity) of the leaves and stunting of the plant, and the collapsed leaves generally remain hanging on the plant for a longer time.

Virus X is widespread throughout the potato-growing areas of the world. Many of the commercial potato varieties grown in North and South America are infected with one or more strains of the virus. Potatoes free from virus X are known to exist including the following registered in Canada: Arran Victory, Avon, Canso, Chippewa, Fundy, Huron, Katahdin, Kennebec, Keswick, Pontiac, Sebago, Sequoia and Teton. Since virus X is not transmitted through

Figures 34, 35.—Symptoms produced by a virulent strain of virus X. 34. Early symptoms (interveinal necrosis and moderate crinkling of lower and middle leaves) in Katahdin. 35. Advanced symptoms (severe necrosis and distortion of all leaves and collapse of lower leaves) in potato seedling.

the true seed, most seedlings are free from this virus. Subsequently, they acquire it sooner or later, depending on their susceptibility and probable chance associations in their early life under commercial conditions (28).

RESISTANT AND IMMUNE SOURCES

The U.S.D.A. 41956, certain of its sibs, and the Saco and Tawa varieties are for practical purposes highly resistant to all the known strains of virus X; certain clones of *Solanum acaule* are also highly resistant (7, 25-27). The nature of the resistance in U.S.D.A. 41956, Saco and Tawa is not completely understood. The varieties of *S. tuberosum* and *S. andigenum,* which are hypersensitive (exhibit top necrosis) to virus X (including the B strain), are highly resistant to the virus in the field. Certain clones of the uncultivated species *S. parodii* Juz. & Buk., *S. curtilobum* Juz. & Buk., and *S. fuzepezukii* Buk. (13) are also hypersensitive to the common strains of virus X.

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VIRUS Y

SYNONYMS

Streak virus Orton; leaf-drop streak virus, Murphy; stipple-streak virus, Atanasoff; acropetal necrosis virus, Quanjer; potato virus 20, J. Johnson; vein-banding virus, Valleau and Johnson; *Solanum virus* 2, Smith; *Marmor upsilon,* Holmes; *Murialba venatenia,* Valleau; *Solanumvirus impermanens,* Roland; and *Maphiflexus solani,* Hansen.

HOST RANGE

AIZOACEAE: *Tetragonia expansa* Murr.; AMARANTHACEAE: *Celosia argentea* L., *Gomphrena globosa* L.; CARYOPHYLLACEAE: *Stellaria media* (L.) Cyrill.; CHENOPODIACEAE: *Beta vulgaris* L., *Chenopodium amaranticolor* Coste & Reyn., *C. urbicum* L., *Spinacia oleraceae* L.; CONVOLVULACEAE: *Convolvulus arvensis* L., *Cuscuta gronovii* Willd.; COMPOSITAE: *Dahlia pinnata* Cav., *Zinnia elegans* Jacq.; LEGUMINOSAE: *Indigofera hirsuta* L., *Vigna sinensis* Endl.; PORTULACACEAE: *Portulaca oleracea* L.; SOLANACEAE: *Browallia, Capsicum, Cyphomandra, Datura* (*D. ferox* L., *D. metel* L., *D. meteloides* Dun.), *Hyoscyamus, Lycopersicum, Lycium, Nicandra, Nicotiana, Petunia, Physalis, Salpiglossis, Schizanthus* and *Solanum,* including *S. acaule* Bitt., *S. aculeatissimum* L., *S. ajuscoense* Buk., *S. elaeagnifolium* Cav., *S. andigenum* Juz. & Buk., *S. boergeri* Buk., *S. brevimucronatum* Hawkes., *S. bulbocastanum* Dun., *S. caldasii* Dun., *S. canariense* Juz. & Buk., *S. capsicastrum* Link, *S. cardiophyllum* Lindl., *S. catarthrum* Juz., *S. chacoense* Bitt., *S. chaucha* Juz & Buk., *S. ciecae* Buk., *S. citrullifolium* A. Br., *S. commersonii* Dun., *S. cordobense* Buk., *S. curtilobum* Juz. & Buk., *S. demissum* Lindl., *S. depexum* Juz., *S. dulcamara* L., *S. edinense* Berth., *S. fendleri* A. Gray, *S. garciae* Juz. & Buk., *S. gibberulosum* Juz. & Buk., *S. goniocalyx* Juz. & Buk., *S. gigantophyllum* Bitt., *S. gracile* Link, *S. guereroense* Corr., *S. horivitzii* Buk., *S. infundibuliforme* Phil., *S. integrifolium* Poir., *S. jamesii* Torr., *S. jasminodes* Paxt., *S. jujuyense* Hawkes, *S. kesselbrenneri* Juz. & Buk., *S. lanciforme* Rydb., *S. macmillanii* Buk., *S. macolae* Buk., *S. maglia* Schlechtd., *S. melongena* L., *S. miniatum* Bernh., *S. megistracrolobum* Bitt., *S. microdontum* Bitt., *S. nigrum* L., *S. nigrum* L. var. *nodiflorum* L., *S. polyadenium* Greenm., *S. parodii* Juz. & Buk., *S. phureja* Juz. & Buk., *S. pinnatisectum* Dun., *S. punae* Juz., *S. raphanifolium* Card. & Hawkes, *S. robustum* Wendl., *S. rybinii* Juz. & Buk., *S. saltense* Hawkes, *S. sambucinum* Rydb., *S. schickii* Juz. & Buk., *S. schreiteri* Buk., *S. simplicifolium* Bitt., *S. soukupii* Hawkes, *S. stenotomum* Juz. & Buk., *S. stoloniferum* Schlechtd., *S. subtilius* Bitt., *S. tuberosum* L., *S. tarijense* Hawkes, *S. verrucosum* Schlechtd., *S. vernei* Bitt. & Wittm., and *S. wittmackii* Bitt.

TRANSMISSION

The virus is transmitted by sap inoculation, by stem and tuber graft and by the following aphids: *Aphis fabae* Scop.; *A. nasturtii* Kltb., *Cavariella pastinacae*

(L), *Macrosiphum euphorbiae* (Thom.), *Macrosiphoniella sanborni* (Gill.), *Myzus certus* (Wlk.), *M. persicae* (Sulz.), *M. ornatus* Laing, and *Neomyzus circumflexus* (Bckt.). The virus is nonpersistent (9, 14, 58, 64, 65).

PHYSICAL PROPERTIES

These properties vary slightly according to the strain. Most of the strains are inactivated by heating at 52° to 62°C. for 10 minutes. The dilution end point ranges from 1:10,000 to 1:50,000 and the longevity in vitro varies from 1 to 18 days at 20° to 22°C. (25, 65). The particles are flexible threads 759 mμ long and 12 mμ wide (7, 13, 24).

IMMUNOLOGICAL AND SEROLOGICAL RELATIONSHIPS

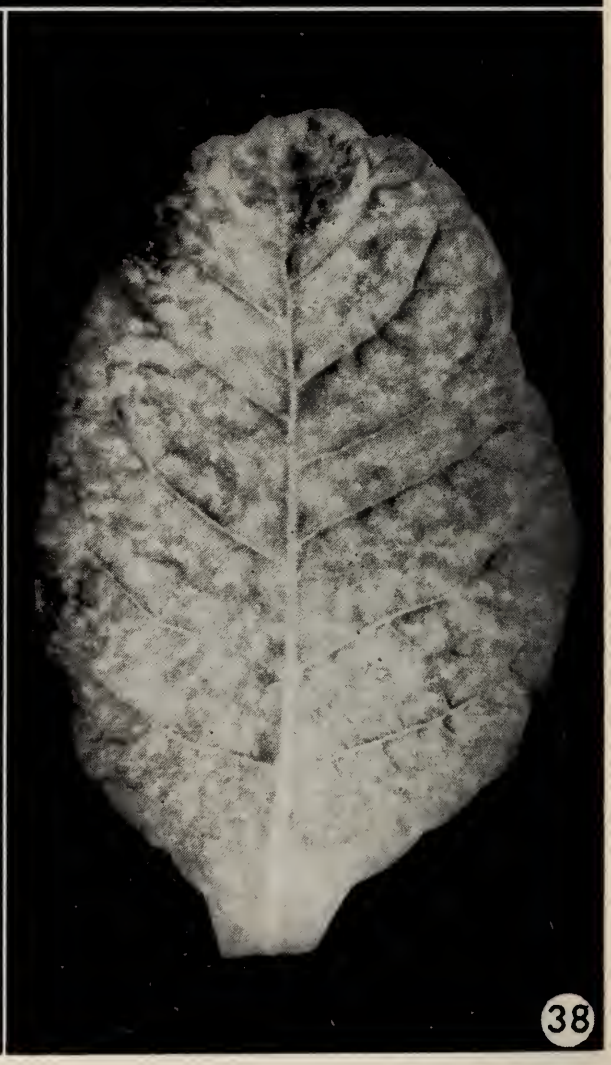
Weak strains of virus Y protect *S. tuberosum, N. tabacum* and other solanaceous plants against the more virulent strains (37, 56). No reciprocal protection is given by strains of virus Y against strains of virus A (8).

An antiserum has been prepared against virus Y, clarified sap or purified suspensions from infected plants of *N. tabacum* being used (9, 11, 15, 16, 24). The antiserum cannot be used satisfactorily for detecting virus Y in potato sap. The best procedure is to transfer the virus to *N. tabacum* and use the infected sap for the serological test. No serological reactions occur between viruses of the A, X and Y groups (8, 16, 28).

INDICATOR HOSTS

The C strain and most of the type strains produce distinctive symptoms in *Nicotiana tabacum*: a bright clearing of the veins of the youngest leaves, and as the leaf grows older a characteristic vein banding (Figures 36, 37). Some strains cause, in addition, a slight crinkling of the youngest leaves. The veinal-necrosis strains produce severe necrosis of the veins and distortion of the leaves in *N. tabacum* (Figure 38). Certain species of *Datura,* including *D. stramonium* and *D. meteloides,* are immune from most strains of virus Y (25) and may be used for separating this virus from others to which these hosts are susceptible. *D. metel* and *D. ferox* are, however, susceptible to several strains of virus Y and react with a vein clearing, puckering and distortion of the youngest leaves (25, 69). Most strains of virus Y produce a vein clearing followed by a vein banding in *Capsicum annuum* (Figure 39).

Some strains of virus Y also produce characteristic local lesions and systemic symptoms in *Chenopodium amaranticolor, C. urbicum, Lycium chinense, L. halimifolium, L. rhombifolium* and *Physalis floridana* (25, 48). In these hosts small, well-defined, dark or brown necrotic lesions are produced at the site of infection. The type of lesion produced in *Lycium halimifolium* is shown in Figure 40. The best results are obtained when carborundum is used as an abrasive and the plants are maintained at 18° to 22° C. The necrotic-fleck strain (61) produces distinctive local necrotic symptoms in *Nicandra physalodes* (60). In this plant the first symptoms are faint necrotic rings, which later develop dark-purple borders and light-green centers. Sometimes these lesions become dark necrotic disks.



Figures 36-38.—Symptoms produced by virus Y in *Nicotiana tabacum* (White Burley). 36. Early symptom (bright clearing of veins). 37. Advanced symptom (vein banding). 38. Necrotic symptoms caused by a veinal necrosis strain of the virus.

Figures 39, 40.—Symptoms caused by virus Y. 39. Advanced symptoms in *Capsicum annuum*. 40. Distinctive local lesions in *Lycium halimifolium*.

Certain strains of virus Y produce barely discernible symptoms or none at all in the following plants: *Gomphrena globosa, Lycopersicum esculentum, Portulaca oleracea, Solanum demissum, S. dulcamara, S. melongena, S. nigum, S. nigrum* L. var. *nodiflorum* and *S. schickii* (30, 45, 54, 65, 72). Virus Y can be separated and differentiated from certain viruses such as viruses A, S and X by being propagated in varieties that are susceptible to it but immune or hypersensitive to the other viruses. Varieties such as Saco, Tawa and U.S.D.A. 41956 will exclude virus X. Saco will also prevent entry of virus S. The varieties British Queen, Canso, Irish Cobbler, Saco and Up-to-Date, which are hypersensitive to virus A, will not accept this virus when it is introduced by the aphid *Myzus persicae*. The shoot pigmentation test described by Martin and Quemener (41) and confirmed by Wenzl (73) indicates the presence of virus Y in certain varieties of potato. The test is based on the fact that the pink or violet pigmentation, which normally occurs uniformly in sprouts on healthy tubers, is irregularly distributed in the sprouts of tubers infected with virus Y.

SYMPTOMS INDUCED IN POTATO

The virus occurs in a number of strains (9, 25, 34, 42), which may produce a variety of symptoms.

Some strains produce barely discernible or no symptoms in varieties such as Arran Banner, Snowdrift (25), Majestic (11), Placid (47) and certain unnamed seedlings (19, 31, 43). When the commoner strains attack certain susceptible varieties they produce symptoms in 3 to 4 weeks. A vein clearing is followed by a blotchy mottling and wrinkling of the leaves in the apical region of the plant (Figure 41). Simultaneously, or later, brownish-black necroses appear along the smaller veins on the undersides of the leaves. These necroses expand, extend along the principal veins and petioles and, eventually, the main stem, where pronounced longitudinal streaks are produced in the collenchyma tissues (Figure 42). Sometimes the necroses penetrate the leaf tissues and appear on the upper surface in the form of irregular flecks that may coalesce, giving the leaf a brownish, rusty appearance. In some cases the leaves in the lower and intermediate positions on the stem become completely necrotic, collapse, fall from the plant or remain hanging by mere strands, giving rise to a distinctive effect known as leaf-drop streak (Figure 43). The virus usually enters the tubers but produces no visible symptoms in them. The yield of affected plants is reduced. In the second and succeeding generations there is usually less foliar necrosis and leaf-drop streak but the plants are dwarfed and brittle, and the leaves severely wrinkled and mottled and closely bunched together. When virus Y is combined with virus X, the symptoms are intensified, producing the disease known as rugose mosaic (Figure 43). The mottling associated with virus Y becomes indistinct when the temperature rises above 26° to 28° C. but the rugosity of the leaves is generally not affected by the change in temperature. The symptoms just described are produced by the common strains in a number of commercial varieties, including Bliss Triumph, Chippewa, Earlaine, Essex, Garnet Chili, Green Mountain, Keswick, McIntyre, President, Pontiac, Red Warba, Russet Rural, Up-to-Date, Warba and White Rose. In Arran Victory, Early Rose, Early Ohio, Epicure, Irish Cobbler, King Edward and Rural New

Figures 41, 42.—Symptoms caused by virus Y. 41. Early symptoms (mottling and rugosity) in apical section of Green Mountain. 42. Systemic symptoms (necrosis of veins and petioles) in potato seedling.

Yorker (Dooley) the common strains react with a marked vein clearing followed by a blotchy mottling, rugosity of the leaves and dwarfing of the plant. Usually any symptom of leaf-drop streak is mild or absent.

Figure 43.—Rugose mosaic (left) and leaf-drop streak (right) produced in Green Mountain by virus Y.

When the common strains attack Katahdin, Kennebec, Majestic, Russet Burbank (Netted Gem), Sebago and Sequoia, these varieties develop irregular, chlorotic or light-green circular lesions on the lower and middle leaves. Later these lesions become necrotic throughout or develop necrotic margins, forming rings that may enlarge, extend to the veins and eventually involve the entire leaf, causing its collapse. The varieties that react in this manner may show no mottling during the season of initial infection and usually develop more leaf-drop streak and a severe rugose mosaic in the second and succeeding generations.

When certain strains of virus Y are introduced to potato by sap inoculation, dark-brown local lesions are sometimes produced on the inoculated leaves. This effect has been reported in a number of varieties and unnamed seedlings (9, 21, 25, 32, 38, 39, 43).

The strain of virus Y now designated as C was originally known as virus C (6, 55). This strain differs from the type strains chiefly in its reactions on certain potato varieties and in not being transmitted by aphids when it is maintained continuously in vegetatively propagated potatoes. However, when strain C is maintained by sap inoculation in series in *Nicotiana tabacum* and *N. glutinosa,* it

becomes transmissible by the aphid *Myzus persicae* (Sulz.) to these and other solanaceous hosts. It loses this capability when it is returned to and maintained in the potato (71). When this strain is introduced by sap inoculation to certain varieties of potatoes, small, circular, dark, necrotic local lesions are produced on the inoculated leaves but there is no systemic invasion. The following varieties react in this manner: Bliss Triumph, British Queen, Craig's Defiance, Duke of York, Early Rose, Epicure, Green Mountain, Irish Cobbler, King Edward, Majestic, President, Russet Burbank (Netted Gem) and Up-to-Date. When strain C is transmitted to the same varieties by graft, a severe top necrosis is produced. This reaction is characterized by the development of circular necrotic lesions on the top leaves; these lesions sometimes coalesce and spread through the entire leaf, causing its collapse. The petioles and stems also develop severe necrotic streaks, which, in certain varieties, result in a destructive leaf-drop streak. In the second and succeeding generations these varieties show a mild to severe mottling and crinkling of the leaves, with only slight necrosis and dwarfing of the plant. Such varieties as Arran Victory, Di Vernon, Great Scot, Katahdin, Kerr's Pink, and U.S.D.A. 41956 react in this manner. The C strain has not been found in potatoes of North American origin but has been reported in the South American species *Solanum andigenum* and *S. stenotomum* (26). It occurs under natural conditions in a number of old European varieties.

A variant of strain C was found in *Solanum jasminoides* (3). In potato this variant produces symptoms that resemble those of strain C, but unlike this strain the variant is readily transmitted by *Myzus persicae* (Sulz.) and retains this capability when maintained continuously in vegetatively propagated susceptible potatoes. Another variant of strain C, also aphid-transmitted, was reported in the Catriona variety (20).

A group of viruses now considered as strains of virus Y were originally described as "necroses das nervuras" (44), potato veinal necrosis virus (65, 66), tobacco veinal necrosis virus (11) and "Virus der Tabak-Rippenbraune" (36). These differ from the type strains in that they produce only faint, transient mottling in some varieties of *Solanum tuberosum* and a necrosis and mottling in *Nicotiana tabacum* resembling that caused by simultaneous infection with certain strains of viruses X and Y (11) (Figure 38). There have also been reported veinal necrosis strains that produce necrotic symptoms resembling those of the type strains in certain varieties of *Solanum tuberosum* (11, 46, 66). Some of the veinal necrosis strains produce only mild and nonnecrotic effects in *Physalis floridana* (46), in which plant the type strains induce varying degrees of necrosis and stunting. Another of these strains causes severe necrotic symptoms in *Petunia hybrida, Capsicum annuum* and *Datura metel* (36), in each of which some of the type strains produce only mild mottling symptoms. Most of the veinal necroses strains have antigen groups in common with the type and C strains, but according to a serological test (5) the necrotic fleck strain found in a South American source (44) is apparently not as closely related to the type strains as the veinal necrosis strains obtained from European sources (11, 13, 36). Furthermore, some of the veinal necrosis strains do not cross-immunize consistently with the type strains (11). However, certain varieties of *Solanum tuberosum* containing the C strain

were found to be strongly protected against invasion by a veinal necrosis strain (46). Most of the veinal necrosis strains are transmitted by the ordinary mechanical means and by the aphid species known to be vectors of the type strains. In addition, one of these strains is transmitted by *Acyrthosiphon pisum* (Harris) (70) and another by *Aphis gossypii* (Glov.) (29). A veinal necrosis strain has also been transmitted by the grasshopper *Tettigonia viridissima* L. (70). Although many of the common varieties of *Solanum tuberosum* do not suffer greatly from the effects of the veinal necrosis strains, potatoes infected with certain of these strains serve as important reservoirs of infection for the tobacco (*Nicotiana tabacum*) crop, in which some of these strains produce a destructive disease (2, 36, 57). Other possible variants of the veinal necrosis group have also been reported (5, 57, 61).

Another group of strains of virus Y causes severe necrotic effects in tomato (22, 54, 62, 63, 68), in which plant most of the type strains produce only a mild, transient vein clearing and vein banding and a slight distortion of the leaves (64). In tomato these strains give rise to a rugosity, diffuse mottling, marked veinal and interveinal necrosis and an upward curling of the leaves. In some varieties a severe leaf-drop streak is produced. Most of these strains are transmitted by *Myzus persicae* (Sulz.). *Macrosiphum euphorbiae* (Thom.) and *Aphis gossypii* (Glov.) have also been reported as vectors of certain of these strains (62, 68).

A strain designated as piedade has also been found in tomato (59). It differs from other strains in that it is nonpathogenic to the potato and causes a distinctive and severe leaf torsion in *Lycopersicum esculentum* var. Marglobe and *L. pimpinellifolium*. It also produces a severe leaf necrosis followed by leaf drop in *Capsicum annuum* and only mild vein clearing and vein banding in *N. tabacum* var. White Burley, *N. glutinosa* and *Petunia hybrida*.

The following plants are also infected by strains of virus Y in the field: *Dahlia* spp. (40), *Capsicum frutescens* (1), *Cyphomandra betacea* (12), *Lycopersicum esculentum* (22, 54, 62), *Physalis angulata* (1), *P. heterophylla, P. virginiana* (25), *Solanum gracile* and *S. nigrum* (1), and *S. nigrum* var. *nodiflorum* (54). When grown near potatoes these hosts may be potential sources of virus Y infection.

RESISTANT AND IMMUNE SOURCES

The following tuber-bearing species of *Solanum* are highly resistant or immune to some of the type strains of virus Y: *Solanum antipoviczii,* and *S. ajuscoense* (67); *S. chacoense, S. catarthrum, S. chaucha, S. commersonii, S. demissum, S. garciae, S. macolae, S. phureja, S. polyadenium,* and *S. rybinii* (21, 51); *S. stoloniferum* (27, 50); and *S. stoloniferum* (reported as *S. longipedicellatum* Bitt.), *S. malinchense* Hawkes, and *S. tlaxcalense* Hawks (49). Certain named varieties that react with a severe necrotic response to virus Y have a strong field resistance to some of the type and C strains (4, 9, 10, 17, 23, 27, 33, 35, 49). The following react in this manner: Canus, Chippewa, Cherokee, Earlaine, Norkota, Nordak, Norgleam, Katahdin, Kennebc, Sebago and Warba. Certain clones of the following species of *Solanum* (in which virus Y produces a necrosis) are proving useful sources of field resistance to some of the type strains of virus Y: *S. simplicifolium*

and *S. vernei* (52), *S. stoloniferum* (50), *S. brevimucronatum, S. jujuyense, S. rybinii* and *S. saltense* (18). Resistance to some of the veinal necrosis strains has been found in certain clones of *S. andigenum, S. commersonii, S. longipedicellatum, S. macmillanii, S. pinnatisectum, S. spectabile and S. simplicifolium* (53).

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CALICO VIRUS
(Alfalfa Mosaic Virus)

SYNONYMS

Potato calico, Hungerford; potato calico virus, Porter; *Solanum virus* 10, Smith; *Marmor medicaginis* Holmes var. *solani*, Black & Price; potato necrosis virus, Oswald; lucerne mosaic virus (N.I.A.B. strain), Richardson and Tinsley.

The calico virus, the potato necrosis virus and the N.I.A.B. strain of the lucerne mosaic virus are now considered strains of the alfalfa mosaic virus (2, 3, 9, 11, 14, 15).

HOST RANGE

AMARANTHACEAE: *Gomphrena globosa* L.; CHENOPODIACEAE: *Beta vulgaris* L., *Chenopodium quinoa* Willd.; COMPOSITAE: *Calendula officinalis* L., *Zinnia elegans* Jacq.; CUCURBITACEAE: *Cucumis sativus* L.; LEGUMINOSAE: *Medicago sativa* L., *M. lupulina* L., *Melilotus albus* Descr., *M. officinalis* Lam., *Pisum sativum* L., *Phaseolus vulgaris* L., *Trifolium hybridum* L., *T. incarnatum* L., *T. pratense* L., *T. repens* L. var. Ladino, *Vicia faba* L., *Vigna sinensis* Endl.; SOLANACEAE: *Capsicum annuum* L., *Datura metel* L., *D. stramonium* L., *Hyocyamus niger* L., *Nicotiana glutinosa* L., *N. rustica* L., *N. sylvestris* L., *N. tabacum* L., *Petunia hybrida* Vilm., *Solanum melongena* L., *S. tuberosum* L.; UMBELLIFERAE: *Apium graveolens* L.

TRANSMISSION

The strains of the alfalfa mosaic virus that attack potato are transmitted by sap inoculation, by stem and tuber graft and by the following species of aphids: *Macrosiphum euphorbiae* (Thom.), *Myzus persicae* (Sulz.) and *Acyrthosiphon pisum* (Harris), (4, 9, 12, 13, 15, 16). The alfalfa mosaic virus, including the calico and tuber necrosis strains, is nonpersistent (15, 18). These strains are frequently spread by aphids from naturally infected alfalfa (*Medicago sativa*) and clover (*Trifolium repens*) when these crops are planted next to potatoes. The viruses are also spread from infected volunteer plants when potatoes follow infected alfalfa and clover crops; they are spread slowly because they survive in only a small percentage of the tubers on infected plants.

PHYSICAL PROPERTIES

Most strains are inactivated by heating at 55° to 60° C. for 10 minutes. The dilution end point ranges from 1:1,000 to 1:2,000 and the longevity in vitro varies from 3 to 4 days at 18° to 20° C. (9, 15, 17). The particles of the virus are rigid rods 550 mμ long and 200 mμ wide (1).

IMMUNOLOGICAL AND SEROLOGICAL RELATIONSHIPS

When susceptible varieties of *Solanum tuberosum*, *Nicotiana tabacum*, and certain other solanaceous hosts are systemically infected with the calico strain, such plants are protected against invasion by the tuber necrosis and other strains (9).

The alfalfa mosaic virus is antigenic. A satisfactory antiserum prepared against the calico and tuber necrosis strains has been made from suspensions of these strains from infected *N. tabacum* plants (10, 15).

INDICATOR HOSTS

A useful plant for distinguishing this virus and its strains is the bean *Phaseolus vulgaris* (9, 15). The calico strain induces in this host, in 36 to 48 hours, irregular reddish-brown local lesions, 4 to 5 mm. in diameter. Later, these lesions develop light-brown, netted centers surrounded by dark-brown necrotic rings. In addition there is a reddening of the veins of the inoculated leaves. The tuber necrosis strain produces similar local lesions, 1 to 2 mm. in diameter, but no reddening of the veins. Occasionally, under cool conditions and subdued light these strains become systemic and cause a necrotic dieback of the tip and main stem of the plant, sometimes resulting in complete collapse and death of the plant. Similar symptoms are produced in cowpea, *Vigna sinensis*.

In *Nicotiana tabacum, Capsicum annuum* and *Solanum nigrum* var. *nodiflorum* the calico strain produces on the inoculated leaves irregular light green or yellow spots, which later become necrotic lesions (Figure 44). In 20 to 25 days systemic symptoms appear; they consist of a bright-yellow mottling, mild necrotic streaking and a vein banding on the leaves (Figure 45). Somewhat similar symptoms are produced in *N. glutinosa*. In these plants the tuber necrosis strain produces similar local lesions but more severe systemic symptoms: necrotic streaking, ring spots and sometimes an oak-leaf mottling (Figure 46). A noteworthy feature is that the infected plants usually recover, the newly formed leaves remaining symptomless. These strains are also carried without symptoms in old plants of *Medicago sativa* and *Pisum sativum,* especially when the plants are grown at high temperatures.

SYMPTOMS INDUCED IN POTATO

As already indicated, there are two main strains of this virus, designated here as the calico and the tuber necrosis strains. A strain called the N.I.A.B. has also been described (15).

The first symtoms of the calico strain appear 15 to 20 days after introduction of the virus. These consist of irregular, bright-yellow or yellowish-white blotches on the lower and middle leaves. The yellowing appears first in the apical section of the leaflet and later extends towards the base. As the plant grows older the symptoms become more intensified, covering large portions of most of the leaves. This yellowing or chlorotic effect gave the disease the name calico (6) (Figure 47). The plants in later generations show symptoms similar to those appearing during the first season. These plants are generally dwarfed, and they gradually degenerate, because the affected leaves lack chlorophyll.

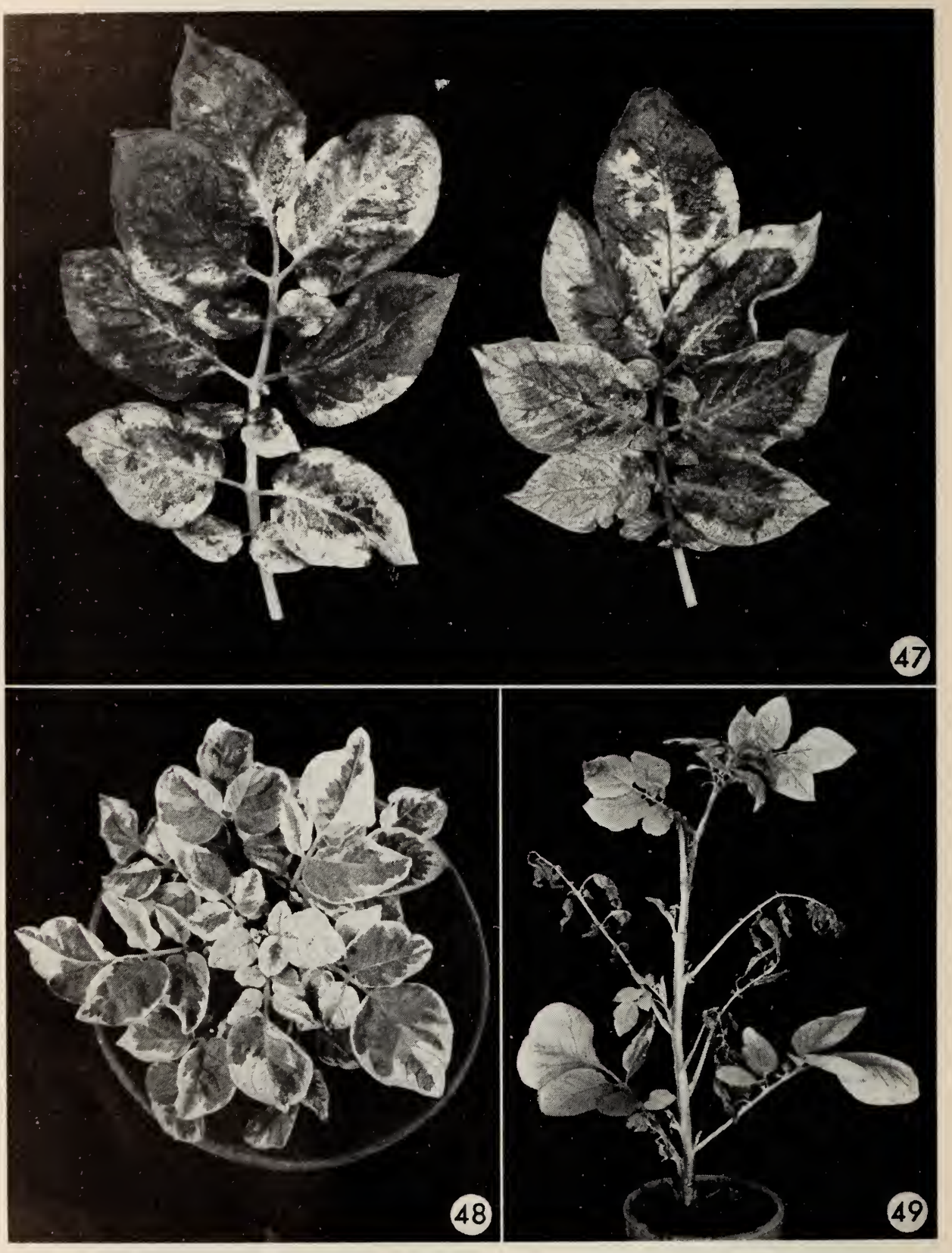
Figures 44-46.—Symptoms caused by the alfalfa mosaic virus. 44. Early symptoms (irregular yellow spots and slight necrosis) produced in *Solanum nigrum* var. *nodiflorum* by the calico strain. 45. Advanced symptoms (bright-yellow mottling and vein banding) produced in *S. nigrum* var. *nodiflorum* by the calico strain. 46. Advanced symptoms (necrosis, ring spots and mottling) produced in *Capsicum annuum* by the tuber necrosis strain.

In some cases when the calico strain is introduced by sap inoculation, local lesions may be produced on the inoculated leaves. Occasionally, too, the lower leaflets on plants mechanically inoculated may develop a brownish necrosis of the tips and margins and a crinkling and stiffening of the leaf blade. When plants are inoculated at temperatures over 26°C., local lesions are produced but the calico or yellowing symptoms may be absent (9). The calico strain does not produce symptoms in the tuber. The following varieties show typical symptoms when infected with the calico strain (9, 15): Arran Victory, Bliss Triumph, Chippewa, Early Ohio, Epicure, Garnet Chili, Green Mountain, Idaho Rural, Irish Cobbler, Katahdin, President, Rural New Yorker (Dooley), Russet Burbank (Netted Gem), Up-to-Date and U.S.D.A. 41956.

A condition in potato that resembles the symptoms of the calico strain is commonly designated variegation (Figure 48). This condition is of nonvirus origin and is due to a heritable genetic abnormality, which sometimes finds expression in only one shoot, or in half of a plant or occasionally in a segment of a leaflet.

The tuber necrosis strain produces severe necrotic effects in the vines and tubers of certain varieties (9). The symptoms appear first on the lowest leaves 6 to 7 days after introduction of the virus. A necrotic browning affects most of the veins, petioles and stems. These symptoms are soon followed by a necrosis of the margins of the leaflets and a yellowing, wilting and collapse of the leaves, which usually remain hanging on the plant (Figure 49), somewhat resembling leaf-drop streak caused by potato virus Y. The necrosis is usually present in the cortical, vascular and pith tissues but not the epidermal layers. The affected tissues (cortical and vascular) assume a rusty-brown color, and irregular brown necrotic patches occur throughout the pith. Necrosis is most severe at the nodes. Sometimes this strain of the virus affects only one shoot or one side of the stem. Occasionally the apical portion of the plant becomes necrotic and collapses before the lower parts are affected, and again the effect is like top necrosis. In about 18 to 20 days systemic symptoms develop on the new leaflets, which become distorted, puckered, and folded upward along the midrib, the tips curving downward. The veins of these leaflets also show a brownish discoloration but no mottling is evident. This stage resembles the secondary phase or rugose mosaic condition caused by potato virus Y. Most of the plants attacked in this manner die prematurely.

The most striking and distinctive symptom produced by the tuber necrosis strain is the necrosis produced in the tubers. When the virus becomes systemic it affects the stolon and enters the tubers, where it produces a necrosis in the cortical tissues just under the epidermis at the stolon end. At this stage the symptoms resemble those characteristic of late blight caused by *Phytophthora infestans* (Mont.) de Bary, because the epidermis over these necrotic masses assumes a purplish or silvery cast. Later, the necrosis extends to all the tissues of the tuber and occurs as deep-brown, dry, corky areas scattered throughout the interior of the tuber. In some cases these necrotic aggregations penetrate the surface, forming irregular and cracked sunken areas that resemble the dry rot produced by certain fungi. These necrotic effects occur in most of the tubers produced on vines that are severely affected. They are usually evident at harvest



Figures 47, 49.—Symptoms caused by the alfalfa mosaic virus. 47. Advanced symptoms of the calico strain in potato seedling. 49. Necrosis, wilting and collapse of leaves caused by a tuber necrosis strain in potato seedling.

Figure 48.—Variegation, a genetic condition, in potato seedling.

time but sometimes do not appear until the tubers have been in storage 4 to 6 weeks. The tuber necrosis resembles that caused by the tuber blotch and Canada streak strains of potato virus F, but differs in that the latter originates in the pith

and usually does not become evident until the affected tubers are in storage 2 to 3 months. The necrosis produced by the tuber necrosis strain in potato is so severe that the virus is self-eliminating because many of the tubers fail to germinate, and when they do, only weak sprouts or stunted plants are produced. The tubers on such plants weigh barely 2 or 3 ounces. The following varieties show the typical symptoms of the tuber necrosis strain: Bliss Triumph, Chippewa, Houma, Katahdin, Mohawk, Pontiac, Teton, White Rose and U.S.D.A. 41956. This strain also attacks Sequoia and Red Warba but does not produce necrosis in the tubers of these varieties.

The tuber necrosis strain is usually most severe when potatoes are planted adjacent to or near fields of alfalfa (*Medicago sativa*) or white clover (*Trifolium repens*), especially Ladino white clover. These leguminous plants are often naturally infected with the tuber necrosis strain and are capable of carrying the virus without symptoms, especially at high temperatures. The strains of the alfalfa mosaic virus that attack potato have been reported from Canada (2, 8), Bulgaria (7), Germany (14), Great Britain (15), Italy (5), Netherlands (10) and the United States (9, 12). The N.I.A.B. strain attacks a number of European varieties, including Craig's Alliance, King Edward and Majestic, but produces in these potatoes faint or no symptoms.

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YELLOW-DWARF VIRUS

SYNONYMS

Potato yellow dwarf, Barrus and Chupp; potato virus 5, J. Johnson; *Solanum virus* 16, Smith; *Marmor vastans,* Holmes; *Aureogenus vastans,* Holmes; *Medicavirus solani,* Hansen.

Strains.—New York: *Marmor vastans* Holmes var. *vulgaris,* Black. *Aureogenus vastans* Holmes var. *vulgaris,* Black. Variant: *Marmor vastans* Holmes var. *lethale,* Black. *Aureogenus vastans* Holmes var. *lethale,* Black. New Jersey: *Marmor vastans* Holmes var. *agalliae,* Black. *Aureogenus vastans* Holmes var. *agalliae,* Black.

HOST RANGE

COMPOSITAE: *Anthemis cotula* L., *Callistephus chinensis* Nees, *Chrysanthemum leucanthemum* L., *Chrysanthemum leucanthemum* L., var. *pinnatifidum* Lecoq. & Lamotte, *Cichorum intybus* L., *Galinsoga ciliata* (Raf.) Blake, *Rudbeckia hirta* L., *Tragopogon porrifolius* L., *T. pratensis* L.; CRASSULACEAE: *Kalanchoe daigremontiana* Hamet & Perrier; CRUCIFERAE: *Barbarea vulgaris* R. Br., *Brassica napus* L., *B. nigra* (L.) Koch, *Capsella bursa-pastoris* (L.) Medic., *Erysimum cheiranthoides* L., *Lepidum campestre* (L.) R. Br., *L. virginicum* L., *Raphanus sativus* L., *Sisymbrium altissimum* L.; LABIATAE: *Leonurus cardiaca* L.; LEGUMINOSAE: *Medicago lupulina* L., *Trifolium agrarium* L., *T. hybridum* L., *T. incarnatum* L., *T. medium* L., *T. repens* L., *T. pratense* L., *Vicia faba* L., *V. sativa* L.; LINACEAE: *Linum usitatissimum* L.; POLYGONACEAE: *Fagopyrum esculentum* Gaertn., *Rumex crispus* L., *R. obtusifolius* L.; SCROPHULARIACEAE: *Verbascum blattaria* L., *V. thapsus* L.; SOLANACEAE: *Datura stramonium* L., *Hyocyamus niger* L., *Lycopersicum esculentum* Mill., *Nicotiana glauca* R. Grah., *N. glutinosa* L., *N. langsdorfii* Weimn., *N. paniculata* L., *N. rustica* L., *N. sanderae* Hort., *N. sylvestris* Speg. & Comes, *N. tabacum* L., *N. undulata* Ruiz & Pav., *Physalis heterophylla* Nees, *P. pubescens* L., *Solanum acaule* Bitt., *S. ajuscoense* Buk., *S. andigenum* Juz. & Buk., *S. antipoviczii* Buk., *S. cardiophyllum* Lindl., *S. melongena* L., *S. neo-antipoviczii* Buk., *S. subexinterruptum* Bitt., *S. tuberosum* L., *S. verrucosum* Schlechtd.; UMBELLIFERAE: *Daucus carota* L. var. *sativa* DC.

TRANSMISSION

The virus is transmissible by sap inoculation to certain solanaceous and nonsolanaceous hosts. It has been transmitted to *Nicotiana glutinosa, N. rustica, N. paniculata, N. tabacum* and *N. undulata*; carborundum was used as an abrasive in the inoculum (4). Preinoculation darkening of the plants and the addition of cysteine hydrochloride (0.01 M to 0.04 M) to the inoculum greatly facilitated transmission of the virus to *Solanum tuberosum, Lycopersicum esculentum, Datura*

stramonium, Nicotiana rustica, Trifolium incarnatum and *Vicia faba* (19). The virus has also been transmitted by pin-puncture into regions where vascular bundles aggregate, such as near the eyes of tubers and in the crowns of certain plants, including *T. incarnatum* and *T. pratense* (5).

The type, or New York, and the New Jersey strains are transmitted by the leafhoppers *Aceratagallia sanguinolenta* (Prov.) and *Agallia constricta* Van D., respectively. *Agallia quadripunctata* (Prov.) transmits both strains (2, 3, 8). The virus is persistent and has survived in the body of the insect for over 150 days (3, 7). The incubation period of the virus in the insect ranges from 6 to 10 days and possibly longer. The virus has been transmitted regularly by the third, fourth and fifth instars of *Aceratagallia sanguinolenta* (7). The New Jersey strain has been transmitted through a small percentage of the oviposited eggs of *Agallia constricta* (11). When the virus was maintained in *T. incarnatum* plants for 12 to 16 years, without insect transmission, it lost its vector transmissibility (10).

The transmission of the yellow-dwarf virus to potato depends largely on the migration of vectors from naturally infected plants such as *T. incarnatum* and *T. pratense* grown near potatoes. Noteworthy, too, is the finding that the virus is not readily disseminated from potatoes infected during the current season (18).

PHYSICAL PROPERTIES

The virus is inactivated by heating at 50° to 53°C. for 10 minutes; the dilution end point ranges from 1:1,000 to 1:10,000 and the longevity in vitro varies from 10 to 13 hours at 23°C. (4, 5, 9). Partially purified concentrates were active after 30 days at 0°C. and the virus survived in the leaves of *Nicotiana rustica* for 7 months at —14°C. (9). The sedimentation constant of the virus (1150S) is larger than that of any other known plant virus (15). Particles as observed in the electron microscope are variable (spheres and short rods ranging from 110 to 290 mμ in diameter and from 30 to 50 mμ in height), indicating considerable morphological complexity (12, 13, 15, 24). The morphology of the particles, but not their infectiousness, was preserved by heat (90°C.) and by such biological fixatives as formaldehyde (1:100) and mercuric chloride (1:1,000 to 1:10,000) (14).

The morphology and infectiousness of purified virus was stabilized by plant sap (*Nicotiana rustica*), sucrose (2.5:100) and a combination of magnesium chloride (0.001 M) and glycine (0.001 M) and certain other cations, amino acids and proteins. The virus retained its morphology longer at pH 6.0 than at pH 8.0. It was most stable between pH 6.0 and pH 8.0 but rapidly lost its infectiousness below pH 6.0 and above pH 8.0 (14).

IMMUNOLOGICAL AND SEROLOGICAL RELATIONSHIPS

The antigenic properties of the virus have not been determined. Mild strains of the virus protected *Nicotiana rustica* plants against invasion by the more virulent strains. None of the mild strains were sufficiently attenuated to be useful for vaccinating potatoes against the field strains (6).

INDICATOR HOSTS

Nicotiana rustica is particularly useful for expressing the symptoms of strains of the yellow-dwarf virus. This plant accepts the virus readily by sap inoculation and has protective factors that augment development of it with the production of distinctive symptoms (6, 14). Similar but less-distinct symptoms are produced in *N. glutinosa*. The strain designated as New York produces in these plants large, diffuse, yellow local lesions, in 25 to 30 days (Figure 50). Later, when the virus becomes systemic, the leaves show a chlorosis and unevenness of the surfaces. In 30 to 40 days, the strain called New Jersey produces fewer and less conspicuous local lesions than those induced by the New York strain. When systemic symptoms appear, there is a marked chlorosis and moderate ruffling of the leaves (6).

A mutant of the New York strain produces in *Nicotiana rustica*, in 25 to 30 days, an extensive necrosis of the veins and petioles, which is followed by an intense chlorosis and later collapse and death of the leaves (Figure 51). Other variants of the virus, which have not been found in nature, produce a variety of symptoms in *Nicotiana rustica*. These range from light-green, diffuse local lesions to more conspicuous yellow lesions with necrotic margins. The systemic symptoms range from a mild chlorosis of the leaves to a more intense yellowing, especially at the tips, vein clearing and scattered yellow or brown necrotic spots on the lamina (6). A post-inoculation temperature of 27 to 30° C. favored the development of both primary and systemic symptoms in *Nicotiana rustica* (19).

Trifolium incarnatum is also a useful plant for distinguishing strains of the yellow-dwarf virus. The New York strain induces in this plant, in 20 to 30 days, a pronounced clearing of the veins of the younger leaves, which is soon followed by a chlorosis and unevenness of the surfaces of these leaves. During the summer

Figures 50, 51.—Symptoms caused by a New York strain of the yellow-dwarf virus in species of *Nicotiana*. 50. Diffuse yellow local lesion on *N. Glutinosa*. 51. Necrotic symptoms on *N. rustica*.

months the chlorosis is sometimes partly replaced by a reddish-brown coloration in the interveinal spaces on both sides of the leaf surfaces. Occasionally the affected plants recover gradually and may show only mild symptoms. The symptoms produced in *Trifolium incarnatum* by the New Jersey strain are variable. They develop first on the older leaves in the form of a rusty-brown necrosis of the veins and petioles. This is usually followed by a chlorosis of the interveinal areas and later collapse of the leaf. If the plant survives the acute stage of infection, it may recover and show only mild symptoms.

SYMPTOMS INDUCED IN POTATO

The strains of the yellow-dwarf virus that attack potato include the two normal or field strains and also certain mutants detected in artificial culture but not in nature (6). The symptoms produced in potato by the two field strains New York and New Jersey are usually similar (6, 19). The disease produced in potato was originally named "yellow dwarf" because of the characteristic yellowing and stunting of the foliage (1). The first symptoms are a slight chlorosis and marginal upward rolling of the leaflets at the apex of the plant (Figure 52). Later the symptoms develop progressively downward, involving most of the leaves on the stem; these leaves eventually assume a pronounced yellowish-green cast with a trace of purpling along the margins and midribs. The affected leaves become brittle and curved upward along the longitudinal axis and change from a yellowish green to a dull yellow and brown as the plant matures. Similar color changes take place in the stems of the plant. In some cases the uppermost leaves become very chlorotic, turn brown and die, giving rise to a type of top necrosis (Figure 53). Generally the affected plants are greatly dwarfed. As the leaf symptoms develop, brownish necrotic flecks appear in the pith of the apical section of the stem of the affected plant. These characteristic internal lesions appear later in the lower sections of the stem, and in the pith and cortex of the nodes and occasionally of the internodes (Figure 54). Flowers rarely appear on diseased plants because the top section is often killed before the blossoms develop. When an inflorescence is affected there is a necrosis of the petals, stamens, sepals and pistil, and a dwarfing of all these parts. Sometimes the affected flowers fail to open. The foliage symptoms are accentuated when the air temperature is above 26° to 28° C. Plants grown at lower temperatures may show less-pronounced symptoms and these may be completely suppressed when the temperature is below 20° C. (26).

A distinctive feature is the effect produced in the tubers. Affected plants generally produce small, misshapen tubers closely appressed to the stem. There are usually deep fissures on the surface and characteristic brown necrotic areas or flecks scattered throughout the pith and outside the vascular ring. In some cases the affected tissues collapse, leaving distinct cavities (Figures 55, 56). Tubers on lightly infected plants may show only a few or no necrotic flecks and outwardly may appear normal. The tubers on infected plants do not always produce diseased plants, and different parts of the same tuber may give rise to healthy and diseased shoots. When the temperature ranges from 16° to 20° C., infected tubers may sprout normally and produce only slightly dwarfed plants.

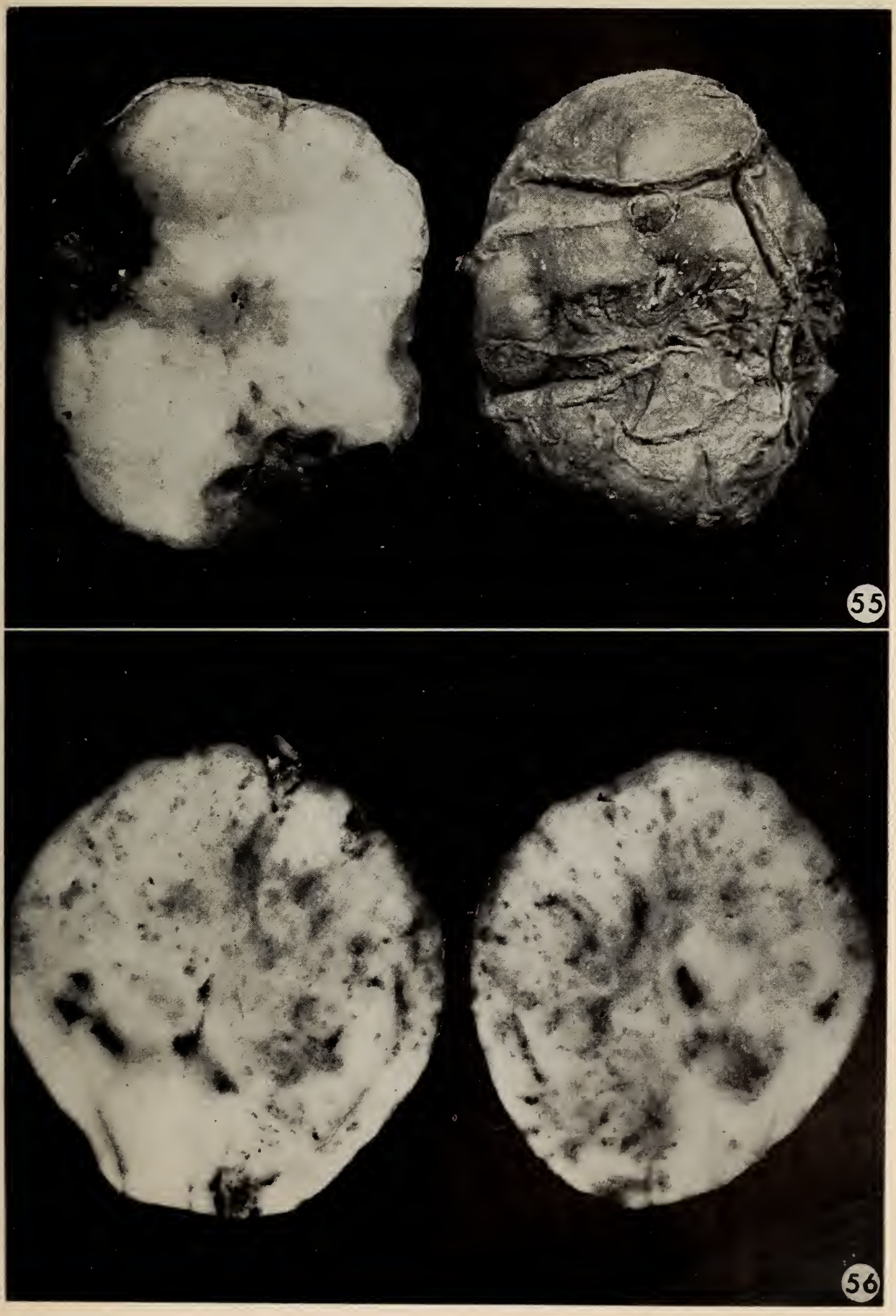
Figures 52-54.—Symptoms caused by a field strain of the yellow-dwarf virus. 52. Early symptoms (slight chlorosis and marginal upward rolling of leaflets) in Katahdin. 53. Top necrosis in Katahdin. 54. Internal necrosis in stems of Rural New Yorker (Dooley).

But emergence is reduced and symptoms are accentuated when the temperature rises to 24° C. At higher temperatures germination is suppressed and the sets may persist in the ground for several weeks and then sprout normally (26).

The symptoms produced in the second and later generations of plants differ from those of the first season (3). The apical section of the plant continues to grow instead of dying, as it usually does, in the primary stage of the disease. The stems are dwarfed and spindly; the leaves are brittle, reduced in size and show a slight interveinal mottling and ruffling (Figure 57). The internal apical necrosis, which marks the onset of the acute stage, may be entirely absent in the secondary stage. Sometimes short, superficial, depressed, necrotic streaks may appear below the leaf axils on the lower part of the stem. This streak may extend some distance out along the lower surface of the petiole, causing the leaves to collapse and fall off the plant (Figure 58). The tubers generally show less malformation and internal necrosis than those produced in the first stage of the disease. Sometimes, because an equilibrium is reached between the virus and the plant, infected potato lines may show only an upward rolling and interveinal mottling of the leaves (Figure 59). Such plants may grow through four or five vegetative generations before becoming completely unproductive. The following varieties show typical symptoms when infected with strains of the yellow-dwarf virus: Bliss Triumph, Chippewa, Columbia Russet, Earlaine, Early Ohio, Early Rose, Green Mountain, Golden, Houma, Katahdin, Keswick, Irish Cobbler, Mesaba, Pontiac, Russet Burbank (Netted Gem), Russet Rural, Rural New Yorker (Dooley), Sebago, Warba, White Rose and a number of unnamed seedlings, (3, 6, 16, 20, 25, 26). The yellow-dwarf virus causes the greatest damage when potatoes are planted near naturally infected hosts. The virus has been found in the following plants in the field: *Barbarea vulgaris, Capsella bursa-pastoris, Chrysanthemum leucanthemum* var. *pinnatifidum, Medicago lupulina, Rudbeckia hirta, Trifolium pratense* and *T. repens* (3, 16-18, 26, 27). The yellow-dwarf virus has been reported as causing serious losses in potatoes in the northern United States and the southern part of Ontario and Quebec (1, 3, 21, 22, 25-27).

RESISTANT AND IMMUNE SOURCES

The varieties Russet Burbank (Netted Gem), Russet Rural, Sebago and Warba have shown a high degree of field resistance to the yellow-dwarf virus. When infected, these varieties show little if any tuber malformation or necrosis or internal necrotic flecking of the stem (20, 23, 25).



Figures 55, 56.—Symptoms caused by the yellow-dwarf virus in Rural New Yorker (Dooley) tubers. 55. Necrotic lesions in interior (left) and deep fissures on surface (right). 56. Severe internal necrotic lesions.

Figures 57-59.—Symptoms caused by the yellow-dwarf virus. 57. Dwarfed, spindly stems and ruffling of leaves produced in second-generation Katahdin by a field strain. 58. Severe symptoms (necrosis and collapse of leaves) in Green Mountain. 59. Chronic symptoms in second and later generations of Rural New Yorker (Dooley). Note diffuse interveinal mottling and slight upward rolling of leaves.

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